MID-CRETACEOUS ANGIOSPERM POLLEN FROM SOUTHERN ENGLAND AND NORTHERN FRANCE

by J. F. LAING

ABSTRACT. Angiosperm pollen grains are described from the Upper Albian to Middle Cenomanian strata of several localities in southern England and northern France. Twenty-two species are described, of which the following thirteen are new: *Psilatricolpites rectilatibus*, *Retitricolpites amplifissus*, *R. crassitransennus*, *R. exiguiexemplum*, *R. meumendum*, *R. promiscuus*, *R. sarthensis*, *R. subtilimaculatus*, *Psilatricolporites complanatius*, *Retitricolporites ecommoyensis*, *R. insolitimorus*, *Triporopollenites curtisi*, and *T. worbarrowensis*. A sequence of angiosperm pollen assemblages is suggested and an attempt is made to relate this to the ammonite zonation.

THE description of angiosperm pollen from the Albian and Cenomanian strata of southern Britain and northern France is important since this is an area which includes the stratotypes of both stages, and where the stratigraphy is understood in detail. Previous studies on early angiosperm pollen assemblages (e.g. Doyle 1969; Pacltová 1971) have generally been concerned with areas where the age of the strata is imprecisely known. This is because correlation with the standard European sequence is impossible, owing to a lack of any suitable marine fossils.

An exception to this is, perhaps, Dettmann's (1973) recent study on the angiosperm pollen from the eastern Australian Albian to Turonian, but here the sequence appears to be rather different from that which occurs in contemporaneous European and North American strata.

The present work represents an attempt to relate the sequence of angiosperm pollen assemblages to the ammonite zonation of the Albian and Cenomanian of north-west Europe, in the hope that it will help other workers to define better the stratigraphy in areas where the mid-Cretaceous sequence occurs in non-marine strata.

LOCATION AND STRATIGRAPHY OF SAMPLES

Samples have been examined from six localities: Lulworth Cove, Worbarrow Bay, Punfield Cove, and Compton Bay on the south coast of England; Saint-Jouin on the coast of Normandy; and Ecommoy near Le Mans. All the samples collected are of marine rocks, except those from Ecommoy which are of a non-marine or brackish facies. The position of each locality is shown on text-fig. 1, and details of each section are given in text-figs. 2–9.

PREPARATION TECHNIQUE

Samples were prepared as follows: crushing; removal of $CaCO_3$ with cold HCl; removal of silicates with cold 60% HF; removal of excess fluorides with warm HCl; removal of remaining minerals by flotation in $ZnBr_2$ solution (SG 2·5); short

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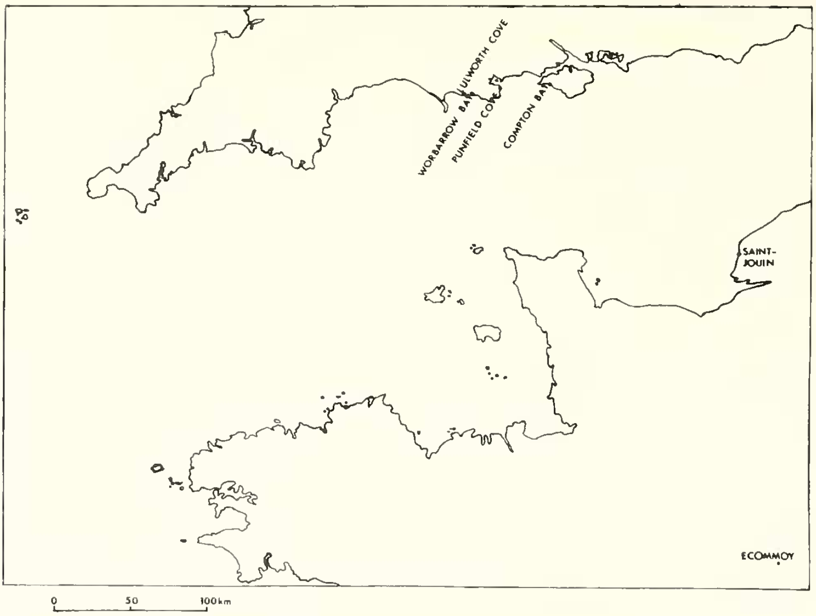


TEXT-FIG. 1. Map showing localities sampled.

centrifuging; up to 30-minutes oxidation with cold concentrated HNO_3; removal of oxidation products with cold 5% NH_4OH for 5 minutes.

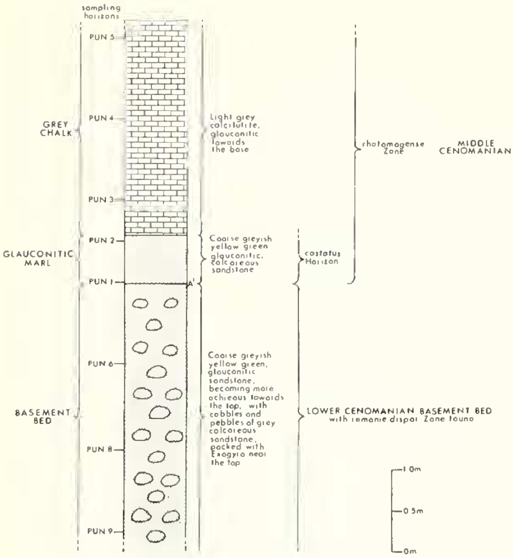
Residues were mounted on cover slips using 'Clearcol', the cover slips then being mounted on slides using 'DePeX'. Excess residues were stored in glycerine (plus a few drops of phenol) in closed plastic vials.

SYSTEMATIC PALYNOLOGY

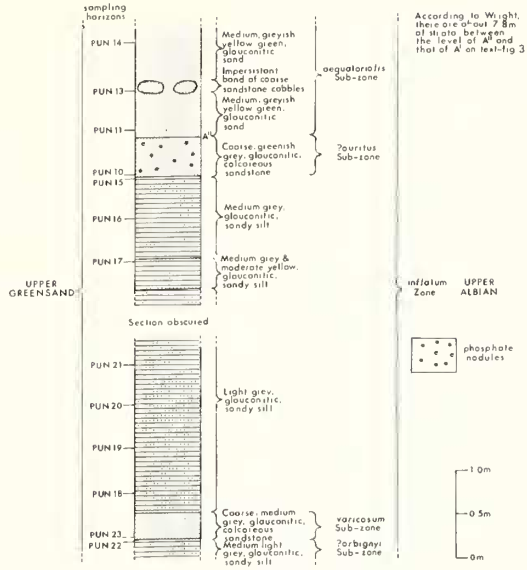
A major problem with early angiosperm palynology is the small size of the pollen grains and of their ornamentation. This difficulty seems to have deterred many authors from producing descriptions of new species which are at all adequate for comparative purposes, with the result that it becomes necessary to create many new species.

Angiosperm pollen is rare in the strata which I have studied, especially so in the marine rocks, and so it has not been possible to base my new species on as many specimens as I would have wished. A further problem is that many of the features of these grains are too small to be measured directly by light microscopy and for this reason I have often had to estimate sizes. Thus where fractions of a micron have been given these are only estimates.

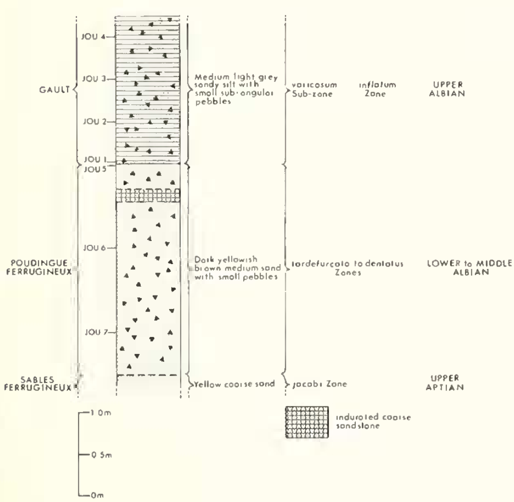
Where I have attributed my specimens to a previously published species, I have used the scheme of graded comparisons proposed by Hughes and Moody-Stuart (1967). When I have given the occurrences of the specimens that I have found, I have done so in terms of the zonal schemes of Spath (1923–1943) for the Albian, and of Kennedy (1969) for the Cenomanian, both summarized on Table 2. When I have referred to the occurrences of other specimens, and to the known ranges of species, the stratigraphic information is generally as stated by the original author; in areas lacking suitable zone fossils, this information may be only approximately correct.



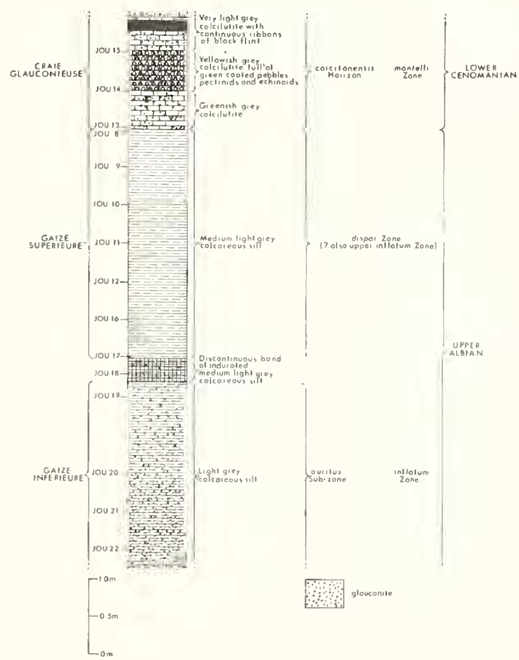
TEXT-FIG. 2. Section at Punfield Cove, Dorset (SZ 045813). (Zonation after Hancock 1969; and Drummond 1970.)



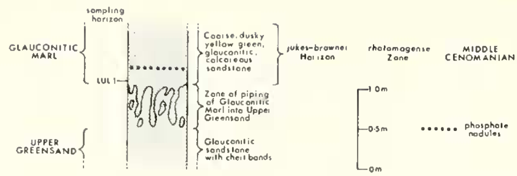
TEXT-FIG. 3. Section at north end of Swanage Bay, Dorset (SZ 043812). Continuation of section at Punfield Cove. (Zonation after Wright, in Arkell 1947.)



TEXT-FIG. 4. Section *c.* 200 m SSW. of steps from Valleuse Boucherot, Saint-Jouin, Seine-Maritime. (Zonation after Juignet 1972.)



TEXT-FIG. 5. Section *c.* 500 m NNE. of steps from Valleuse Boucherot, Saint-Jouin, Seine-Maritime. (Zonation after Juignet 1972.)



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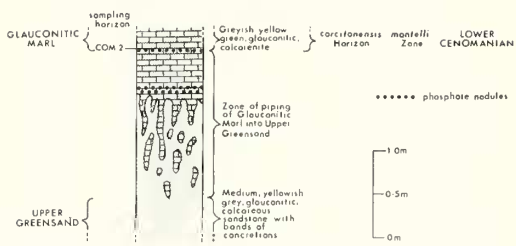

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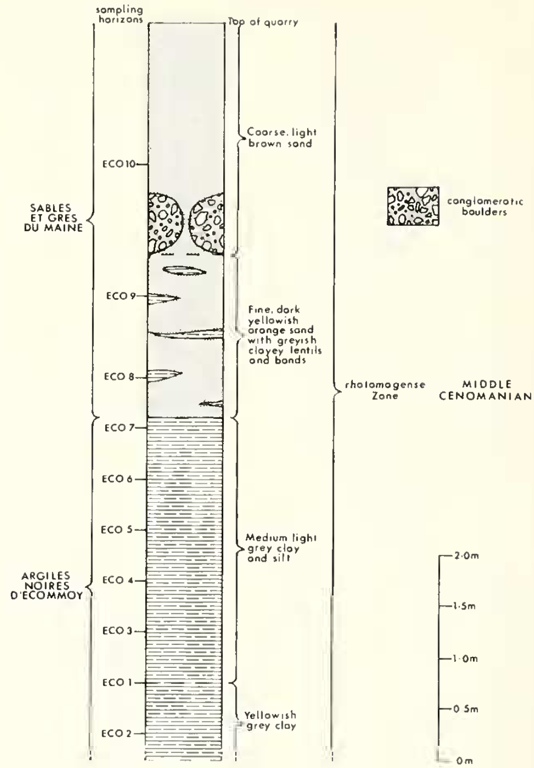


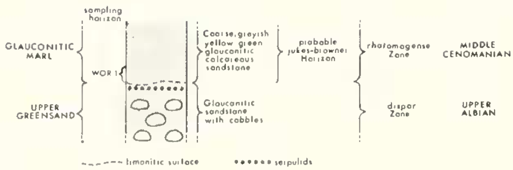
Text-fig. 9.

TEXT-FIG. 6. Section at Lulworth Cove, Dorset (SY 825800). (Zonation after Hancock 1969.)

TEXT-FIG. 7. Section at Compton Bay, Isle of Wight (SY 366853). (Zonation after Kennedy 1969.)

TEXT-FIG. 8. Section at Worbarrow Bay, Dorset (SY 862804). (Zonation after Wright, in Arkell 1947; and Kennedy, pers. comm.)

TEXT-FIG. 9. Section at Carrière de Bezonnais, Ecommoy, Sarthe. (Zonation after Juignet and Médus 1972.) Palynological comparisons with the marine sequence suggest the Argiles noires to be of approximately lower Middle Cenomanian age (Laing 1973.)



Text-fig. 8.

The following abbreviations are used in the text:

D	depth	NT	nexine thickness
DC	depth of colpus (colpi)	OA	oblique aspect
E	equatorial aspect	P	polar aspect
ED	equatorial diameter	PD	polar diameter
ET	exine thickness	s	standard deviation
L	length	ST	sexine thickness
LC	length of colpus (colpi)	W	width
LD	diameter of lumina of microreticulum	WC	width of colpus (colpi)
MW	width of muri of microreticulum		

The occurrence of each species in each horizon and locality is summarized on Table 1.

All specimens are deposited in the Sedgwick Museum, Cambridge, where a catalogue of specimens may also be found on 'Taxon Register' forms (form 6109). Co-ordinates given are for Leitz Dialux microscope no. 469843, also in the Sedgwick Museum. Specimens shown in scanning electron micrographs are located according to the co-ordinate reference system described by Laing (1974).

Anteturma POLLENITES Potonié, 1931
Turma PLICATES Naumova emend. Potonié, 1960
Subturma MONOCOLPATES Iversen and Troels-Smith, 1950
Genus ASTEROPOLLIS Hedlund and Norris, 1968

1968 *Asteropollis* Hedlund and Norris, p. 152.

Type species. Asteropollis asteroides Hedlund and Norris, 1968, p. 153, pl. 6, figs. 18–20; pl. 7, figs. 1–5.

Comments. Hedlund and Norris originally placed this genus in the subturma Polyptyches. However, I consider that it is better regarded as being a monosulcate form and I have accordingly transferred it to the subturma Monocolpates.

CfB. *Asteropollis asteroides* Hedlund and Norris, 1968

Plate 94, figs. 12–14

1968 *Asteropollis asteroides* Hedlund and Norris, p. 153, pl. 6, figs. 18–20; pl. 7, figs. 1–5.

Description of five specimens from samples ECO3 and ECO 5. Sub-circular to circular in polar view, semicircular in equatorial view. Tri-, tetra-, penta-, or hexachotomosulcate; sulcus margins poorly defined and rather ragged. Clear exine stratification into unstructured nexine and microreticulate sexine; sexine usually thicker than nexine (occasionally nexine thicker than sexine); sexine shows no tendency to detach from nexine. Microreticulum usually slightly imperfect (occasionally perfect) with some discrete clavae present; lumina all of about the same size; sexine absent in patches over surface of sulcus.

Dimensions. ED 21–26 μm (5), PD 13 μm (1), ET 1·2–1·5 μm (5), NT 0·5–0·8 μm (5), ST 0·5–1·0 μm (5), ST/NT 0·6–2·0 (5), LD 0·2 μm (5), MW 0·1–0·2 μm (5), sulcus diameter 15–20 μm (5), sulcus diameter/ED 0·7–0·8 (5), L rays of sulcus/sulcus diameter 0·2–0·4 (5), W rays of sulcus/sulcus diameter 0·2–0·4 (5).

Orientation. P 80·0%, E 20·0%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *costatus* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrences: Hedlund and Norris (1968), Middle Albian, Oklahoma; Dettmann (1973), Cenomanian and Turonian, eastern Australia. *Known range*: Middle Albian to Turonian.

Comments. My attribution of these specimens to this species strictly requires an emendation of the genus, which should only include tetra- and pentachotomosulcate forms according to Hedlund and Norris's diagnosis. However, I am reluctant to make any formal emendation based on the few specimens which I have seen. The form described by Hedlund and Norris also differs in having the nexine slightly thicker than the sexine.

Genus LILIACIDITES Couper, 1953

1953 *Liliacidites* Couper, p. 56.
1958 *Clavatipollenites* Couper, p. 159.
1961 *Retimonocolpites* Pierce, p. 47.

Type species. Liliacidites kaitangataensis Couper, 1953, p. 56, pl. 7, fig. 97.

Comments. Couper (1953) proposed the genus *Liliacidites* for monosulcate pollen grains with reticulate exines, adding that the genus be for the reception of pollen of liliaceous affinity which cannot be more accurately placed. The same author (1958) proposed the genus *Clavatipollenites* for monosulcate grains with a sexine of clavate projections which tend to expand and fuse at their tips to form a tectate exine. Couper made no suggestion as to how this genus was to be distinguished from *Liliacidites*. Kemp (1968) noted the morphological similarity of the two genera but implied that *Liliacidites* be used for grains of unquestionable angiospermous origin, whereas *Clavatipollenites* should be retained as a separate genus for forms of a more questionable affinity. In my opinion, such a distinction, based on the supposed affinity of a dispersed grain, has no place in palaeopalynology and any distinction should be made on morphological grounds.

Dettmann (1973) attempted such a morphological distinction. She proposed that *Liliacidites* should include forms with a differentially thickened exine and a sulcus clearly formed in both the nexine and sexine. *Clavatipollenites* was proposed to include forms with an exine of uniform thickness in which the sulcus is invariably developed in the nexine but only occasionally in the sexine. I do not think that the question of the presence or absence of differential exine thickening is sufficiently important a character to justify the distinction of two genera. As for the question of the development of the sulcus in the sexine, the holotype of the type species of *Clavatipollenites*, *C. hughesii*, clearly has the sulcus developed in both the nexine and sexine. This is also the case with *C. rotundus* Kemp, which Dettmann seems prepared to leave in the genus *Clavatipollenites*. Thus, I do not think that the degree of development of the sulcus in the sexine is a valid feature for the distinguishing of these two genera. I am thus of the opinion that no useful purpose is served by the retention of *Clavatipollenites* as a genus separate from *Liliacidites*.

CfA. *Liliacidites peroreticulatus* (Brenner) Singh, 1971

Plate 93, figs. 2–5

1963 *Peromonolites peroreticulatus* Brenner, p. 94, pl. 41, figs. 1–2.
1971 *Liliacidites peroreticulatus* (Brenner) Singh, p. 188, pl. 28, figs. 6–11.

Description of twenty-one specimens from samples ECO 2, ECO 4, and ECO 5. Oval in polar view; semi-circular to oval, sub-circular or circular in equatorial view. Monosulcate; sulcus parallel-sided or gaping with pointed ends; sexinal margins usually entire (occasionally slightly ragged); nexinal margins entire, often slightly infolded. Clear exine stratification into unstructured nexine and microreticulate sexine, which are often partially or completely separated from each other by a cavity; where separation has not occurred, the sexine is attached to the nexine by bacula, the muri being swollen over the point of attachment. Microreticulum perfect, lumina of varying size and of irregularly polygonal shape.

Dimensions. L (whole grain) 17 (20·4) 26 μm (15), L (nexinal inner body) 14 (17·4) 21 μm (15), W (whole grain) 13 (18·8) 23 μm (17), W (nexinal inner body) 10 (15·2) 21 μm (17), D (whole grain) 12–19 μm (6), D (nexinal inner body) 10–20 μm (6), L/W (whole grain) 1·0–1·6 (6), L/W (nexinal inner body) 1·0–1·9 (6), ET (where nexine and sexine are still in contact) 1·0 (1·6) 2·0 μm (21), NT 0·5 (0·7) 1·0 μm (21), ST 0·5 (0·8) 1·0 μm (21), ST/NT 0·5 (1·2) 2·0 (21), LD (least) 0·2 (0·8) 1·5 μm to (greatest) 1·5 (2·5) 4·0 μm (21), MW 0·2 (0·4) 1·0 μm (21), sulcus L 12–18 μm (8), sulcus L/L (whole grain) 0·7–0·9 (8), sulcus W 0·5 (2·8) 11·0 μm (19), sulcus W/W (whole grain) $<$ 0·1 (0·2) 0·5 (15), sulcus D 0·5 (2·1) 5·0 μm (14), sulcus D/D (whole grain) $<$ 0·1–0·3 (6).

Orientation. P 38·1%, equatorial transverse aspect 28·6%, equatorial longitudinal aspect 0·0%, OA 33·3%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *costatus* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrences: Brenner (1963), Upper Barremian to Albian, Maryland; Norris (1967), Late Albian to ?Cenomanian, Alberta; Brenner (1968), Albian, Peru; Agasie (1969), Cenomanian, Arizona; Singh (1971), Middle to Upper Albian, Alberta; Azéma, Durand and Médus (1972), Middle Cenomanian, France. *Known range*: Upper Barremian to Cenomanian.

TABLE 1. Presence (+) or absence (−) of individual species at each locality and horizon. A, *inflatum* Zone, Punfield Cove; B, *inflatum* Zone, Saint-Jouin; C, *dispar* Zone, Saint-Jouin; D, *carcitanensis* Horizon, Saint-Jouin; E, *carcitanensis* Horizon, Compton Bay; F, *costatus* Horizon, Punfield Cove; G, *jukes-brownei* Horizon, Worbarrow Bay; H, *jukes-brownei* Horizon, Lulworth Cove; I, Argiles noires of Ecommoy.

Locality	A	B	C	D	E	F	G	H	I
A. asteroides	−	+	−	−	−	+	−	−	+
L. peroreticulatus	+	+	−	+	+	+	−	−	+
L. rotundus	+	+	+	+	+	+	−	−	+
P. erugatus	−	−	−	−	+	−	−	−	+
P. rectilatibus	−	−	+	−	−	−	+	+	+
R. amplifissus	−	+	+	+	+	−	+	+	+
R. crassitransennus	−	−	−	−	−	−	+	+	+
R. exiguiexemplum	−	+	+	−	−	+	−	−	+
R. georgensis	−	+	−	+	+	+	+	+	+
R. meumendum	−	+	+	−	−	−	−	−	+
R. nemejci	−	−	+	−	−	−	−	−	+
R. promiscuus	−	+	+	+	−	+	+	−	+
R. sarthensis	−	+	−	+	−	+	+	−	+
R. subtilimaculatus	−	+	−	−	+	−	−	−	+
Retitricolpites sp 1	+	+	−	−	+	+	−	−	+
S. sarstedtensis	−	+	+	−	−	+	−	−	+
P. complanatius	−	−	−	−	+	+	−	−	+
R. ecommoyensis	−	+	−	−	+	+	+	−	+
R. insolitimorus	+	−	+	+	+	+	−	+	+
C. subtilis	−	−	−	−	−	−	+	−	−
T. curtisi	−	−	−	−	−	−	+	−	−
T. worbarrowensis	−	−	−	−	−	−	+	−	−

Comments. Distinction from *L. rotundus* (Kemp) is sometimes a little difficult. Generally, however, *L. rotundus* has a finer-meshed microreticulum with narrower muri, and has the muri composed of bacula or clavae rather than being supported by bacula.

Brenner (1963) described two similar species from the Potomac Group, *Peromonolites reticulatus* and *P. peroreticulatus*, stating that they were distinguishable on the basis of grain size and lumen diameter. However, the specimens found in the present study overlap the ranges for these characters of both of Brenner's species. I have examined some material from the Patapsco Formation of the Potomac Group and have found that these species differ as follows: *P. peroreticulatus* has more or less polygonal lumina and muri with a beaded surface, whereas *P. reticulatus* has more sinuous muri, such that the lumina are not so polygonal, the muri having smooth surfaces.

CfB. *Liliacidites rotundus* (Kemp 1968) comb. nov.

Plate 90, figs. 1-6

1963 *Liliacidites dividuus* (Pierce) Brenner, p. 93, pl. 40, figs. 7-10.
1968 *Clavatipollenites rotundus* Kemp, p. 424, pl. 79, figs. 1-19; pl. 80, figs. 1-8; text-fig. 2.

Description of seven specimens from samples JOU 3 and JOU 4. Oval to sub-circular in polar view, oval in equatorial longitudinal view, sub-circular or oval in equatorial transverse view. Monosulcate, sulcus slit-like or gaping, margins entire. Clear exine stratification into unstructured nexine and microreticulate sexine composed of clavae or bacula, sexine occasionally tending to detach from nexine. Microreticulum perfect, lumina generally of varying size (very rarely of more uniform size) and irregularly polygonal shape. Grain outlines generally finely indented (sometimes almost smooth).

Dimensions. L 18–29 μm (4), W 16–22 μm (4), D 14–22 μm (4), L/W 1·1–1·3 (2), D/W 0·7–1·2 (2), L/D 1·1 (1), ET 1·5–2·5 μm (7), NT 0·5–1·5 μm (7), ST 0·9–1·0 μm (7), ST/NT 0·7–2·0 (7), LD (least) 0·1–0·3 μm to (greatest) 0·3–1·5 μm (7), MW 0·2–0·3 μm (7), sulcus L 13–22 μm (4), sulcus L/L 0·7–0·8 (4), sulcus W 2–10 μm (4), sulcus W/W 0·1–0·5 (4), sulcus D 1–9 μm (4), sulcus D/D 0·1–0·6 (4).

Orientation. P 28·6%, equatorial transverse aspect 28·6%, equatorial longitudinal aspect, 14·3%, OA 28·6%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *costatus* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrences: Brenner (1963), Albian, Maryland; Hedlund (1966), Cenomanian, Oklahoma; Brenner (1967), Cenomanian, New Jersey; Hedlund and Norris (1968), Middle Albian, Oklahoma; Kemp (1968, 1970), Lower Albian (?*tardefurcata* Zone) to Upper Albian, England; Habib (1969), Middle Cretaceous, sea bed near the Bahamas; Playford (1971), Albian, Saskatchewan and Manitoba; Singh (1971), Albian to Cenomanian, Alberta; Azema, Durand and Médus (1972), Middle Cenomanian, France. *Known range*: ?*tardefurcata* Zone, Lower Albian to Cenomanian.

EXPLANATION OF PLATE 90

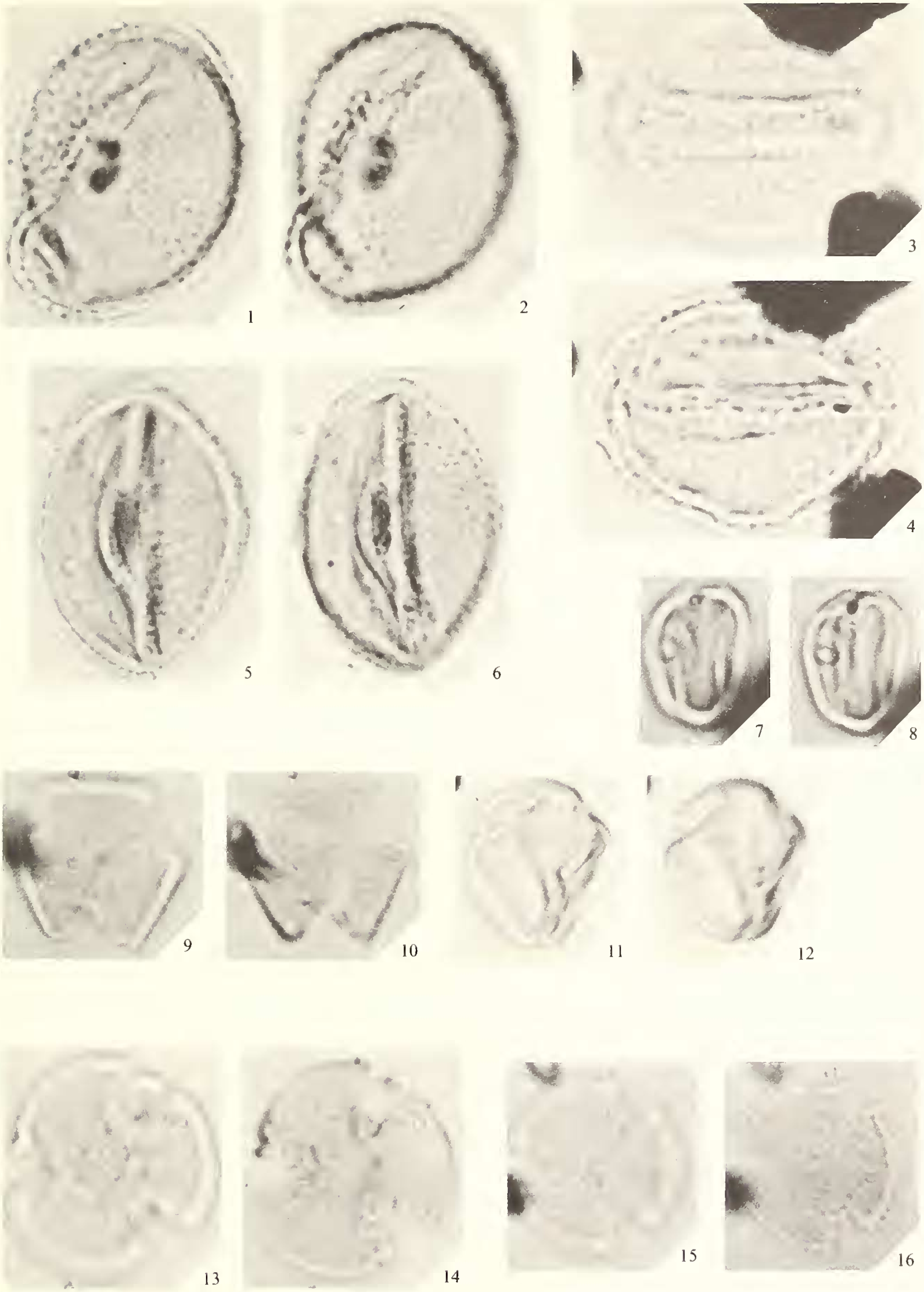
All figures × 2000.

Figs. 1–6. CfB. *Liliacidites rotundus* (Kemp). 1–2, oblique aspect; JOU 4, JL 169.1; 26.9, 106.9; 1, median focus; 2, low focus. 3–4, specimen with sexine partially detached from nexine; distal polar aspect; JOU 12, JL 177.1; 25.6, 104.6; 3, high focus; 4, median focus. 5–6, specimen with darkened sulcus borders; proximal polar aspect; ECO 6, JL 188.2; 24.1, 098.9; 5, median focus; 6, low focus.

Figs. 7–8. CfC. *Psilatricolpites erugatus* (Hedlund). Near equatorial aspect; ECO 5, JL 187.3; 34.1, 108.3; 7, high focus; 8, median focus.

Figs. 9–12. *Psilatricolpites rectilatibus* sp. nov. 9–10, holotype; polar aspect: ECO 5, JL 187.2; 59.0, 110.8; 9, high focus; 10, median focus. 11–12, oblique aspect; ECO 5, JL 209.3; 35.6, 101.2; 11, median focus; 12, high focus.

Figs. 13–16. *Retitricolpites amplifissus* sp. nov. 13–14, holotype; oblique aspect; ECO 5, JL 209.2; 40.8, 096.6; 13, high focus to show ornament; 14, median focus. 15–16, small specimen; polar aspect; ECO 5, JL 187.3; 41.4, 097.0; 15, high focus to show ornament; 16, median focus.



LAING, angiosperm pollen

Comments. See comments for *L. peroreticulatus* for distinction from this species. Kemp (1968) attempted to distinguish this species from *Liliacidites* (al. *Clavatipollenites*) *hughesii* (Couper 1958, p. 159, pl. 31, figs. 19–22 emend. Kemp 1968, p. 426, pl. 80, figs. 9–19) comb. nov. on the basis of size-range and shape. However, I have found that the two species seem to show too great an overlap in the ranges of these characters to allow a reliable distinction to be made on this basis. Kemp further suggested that the nature of the sulcus could be used to differentiate the species, the sulcus having entire margins with darkened borders in *L. rotundus*, and being indistinct or with ragged margins and no darkened borders in *L. hughesii*. Although I have found a few specimens of *L. rotundus* with darkened sulcus borders (e.g. Pl. 90, figs. 5–6), it is the exception in the specimens that I have observed; furthermore, the holotype of *L. hughesii* has a distinct sulcus with entire margins. Thus I do not consider that the nature of the sulcus should be used as a distinguishing character. In my opinion the most useful distinguishing character is (as Kemp also stated) the degree of development of the microreticulum, it being perfect in *L. rotundus* and imperfect in *L. hughesii*.

Retimonocolpites dividuus Pierce, 1961, was poorly described and figured. Pierce did, however, state that the aperture (i.e. sulcus) almost encircles the grain, dividing it into two hemispheres; on the basis of this feature, Pierce's species seems to be distinct. Brenner (1963) and later authors (Hedlund 1966; Hedlund and Norris 1968; Brenner 1967; Habib 1969; and Singh 1971) described or figured forms identified as Pierce's species, which seem to more closely resemble *L. rotundus*.

Subturma TRIPTYCHES Naumova emend. Potonié 1960

Several genera have been used by various authors for early tricolpate pollen. I find the genera of van der Hammen (1956) the most convenient, at least for light microscope studies. For S.E.M. studies, different genera may be preferred based on the greater structural variation which can be observed, and for practical purposes it may become necessary to have separate taxonomies for each mode of observation (in which case the S.E.M. taxonomy will probably be the correct 'formal' one, and the light microscope taxonomy will be rather more informal).

Genus PSILATRICOLPITES van der Hammen ex van der Hammen and Wymstra, 1964

1956 *Psilatricolpites* van der Hammen, p. 88.
1964 *Psilatricolpites* van der Hammen ex van der Hammen and Wymstra, p. 234.

Type species. Psilatricolpites clarissimus (van der Hammen) emend. van der Hammen and Wymstra, 1964, p. 235, pl. 2, fig. 2.

CfC. *Psilatricolpites erugatus* (Hedlund 1966) comb. nov.

Plate 90, figs. 7–8

1966 *Tricolpites erugatus* Hedlund, p. 30, pl. 9, fig. 2a–b.
1967 *Psilatricolpites parvulus* (Groot and Penny) Norris, p. 107, pl. 17, figs. 5–6.

Description of thirty-two specimens from samples ECO 1, ECO 3, ECO 4, ECO 5, and ECO 7. Perprolate to prolate (very occasionally prolate spheroidal); elliptical in equatorial view. Three distinct (occasionally indistinct) slit-like (occasionally more gaping) colpi with entire (occasionally more ragged) margins. No clear exine stratification. Psilate.

Dimensions: PD 10 (12·2) 17 μm (27) s2·0 μm, ED 5 (7·6) 11 μm (32) s1·4 μm, PD/ED 1·1 (1·6) 2·3 (27), ET 0·2 (0·7) 1·1 μm (32), LC 7 (9·1) 13 μm (27), LC/PD 0·5 (0·7) 0·9 (27).

Orientation. P 0·0%, E 84·4%, OA 15·6%.

Occurrence. This study: *carcitanensis* Horizon, *mantelli* Zone, Lower Cenomanian to *rhotomagense* Zone (?*costatus* Horizon), Middle Cenomanian. Other occurrences: Hedlund (1966), Cenomanian, Oklahoma; Norris (1967), Late Albian, Alberta; Singh (1971), Upper Albian and Cenomanian, Alberta; Azema, Durand and Médus (1972), Middle Cenomanian, France. *Known range*: Upper Albian and Cenomanian.

Comments. It is difficult to decide whether this form is more closely referable to *Tricolpopollenites parvulus* Groot and Penny, 1960 or *Tricolpites erugatus* Hedlund, 1966. Groot and Penny's description of *T. parvulus* stated 'grains about isodiametric, usually seen in polar view', which seems to suggest that this species should have a spheroidal shape (although one of Groot and Penny's figures, pl. 42, fig. 9, shows a clearly prolate form). Norris (1967) did not describe this species but, of the two specimens which he figured, one is prolate and the other more or less spheroidal. The forms described as *Psilatricolpites parvulus* by Singh (1971) are 'sub-prolate to almost isodiametric'. I have placed the specimens that I have found in Hedlund's species since this definitely includes prolate forms. However, Hedlund included both smooth and microgranulose specimens in this species, and the latter condition has not been observed in the specimens found in the present study.

P. rectilatibus sp. nov. differs by generally having a greater equatorial diameter and a more spheroidal or oblate shape. It also seems to be more deeply trilobate.

Psilatricolpites rectilatibus sp. nov.

Plate 90, figs. 9–12

Description of fourteen specimens from samples ECO 5 and ECO 7. Spheroidal to oblate; deeply trilobate, more or less straight-sided triangular outline in polar view. Three distinct long slit-like or gaping colpi generally with entire margins, angul-aperturate. No clear exine stratification. Psilate.

Holotype. Sample ECO 5, slide JL 187.2; 59.0, 110.8. Plate 90, figs. 9–12. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. ED 10 (12·1) 15 μm (14), ET 0·2 (0·7) 1·0 μm (14), WC 0·2 (2·6) 5·0 μm (4), WC/ED < 0·1 (0·2) 0·4 (4), DC 0·1 (1·6) 3·0 μm (4), DC/ED < 0·1 (0·1) 0·2 (4).

Orientation. P 28·6%, E 0·0%, OA 71·4%.

Occurrence. This study: *dispar* Zone, Upper Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. *Tricolpopollenites parvulus* Groot and Penny, 1960 was not described adequately enough to allow a close comparison; it does seem, however, to differ from this species in having short colpi. *Tricolpites pachyexinus* Couper, 1953 differs by being larger, by having a much thicker exine and by occasionally being tetracolpate. *T. gillii* Cookson, 1957 differs by being larger and by having a finely granular tectate exine. *Tricolporopollenites triangulus* Groot, Penny and Groot, 1961 differs by having pores. *Psilatricolpites tetradus* Brenner, 1968 differs by having a more circular amb, exine stratification, and by most commonly occurring in tetrads. See comments for *P. erugatus* for distinction from this species.

Genus RETITRICOLPITES van der Hammen ex van der Hammen and Wymstra, 1964

1956 *Retitricolpites* van der Hammen, p. 90.
1964 *Retitricolpites* van der Hammen ex van der Hammen and Wymstra, p. 234.

Type species. Retitricolpites ovalis van der Hammen and Wymstra, 1964, p. 234, pl. 1, figs. 5-6.

Retitricolpites amplifissus sp. nov.

Plate 90, figs. 13-16; Plate 91, figs. 1-2

1968 *Tricolpites* sp. 2 Kemp, p. 432, pl. 81, figs. 23-24.

Description of sixteen specimens from samples ECO 3, ECO 4, ECO 5, and ECO 7. Oblate, perhaps to spheroidal; circular to sub-triangular, deeply trilobate outline in polar view. Three distinct, quite short colpi which gape at the equator, margins entire to ragged. Clear exine stratification into unstructured nexine and microreticulate sexine; sexine of equal thickness to, or more commonly thicker than, nexine. Microreticulum most commonly perfect, but sometimes imperfect; lumina generally of varying size (but sometimes of fairly constant size) and irregularly polygonal in shape. Some specimens with a smooth inner central body (see Pl. 91, figs. 1-2). Grain outlines finely indented.

Holotype. Sample ECO 5, slide JL 209.2; 40.8, 096.6. Plate 90, figs. 13-14. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. Type material: ED 11 (19·9) 27 μm (16), ET 1·0 (1·3) 2·0 μm (16), NT 0·2 (0·5) 1·0 μm (16), ST 0·5 (0·9) 1·0 μm (16), ST/NT 0·9 (2·1) 5·0 (16), LD (least) 0·1 (0·2) 0·8 μm to (greatest) 0·1 (0·9) 1·5 μm (16), MW 0·1 (0·2) 0·3 μm (16), WC 2·0 (4·9) 8·0 μm (8), WC/ED 0·1 (0·2) 0·3 (8), DC 2·0 (4·9) 9·0 μm (8), DC/ED 0·1 (0·2) 0·3 (8). Other material: Sample JOU 4, ED 15-23 μm (6); Sample JOU 15, ED 16-22 μm (5).

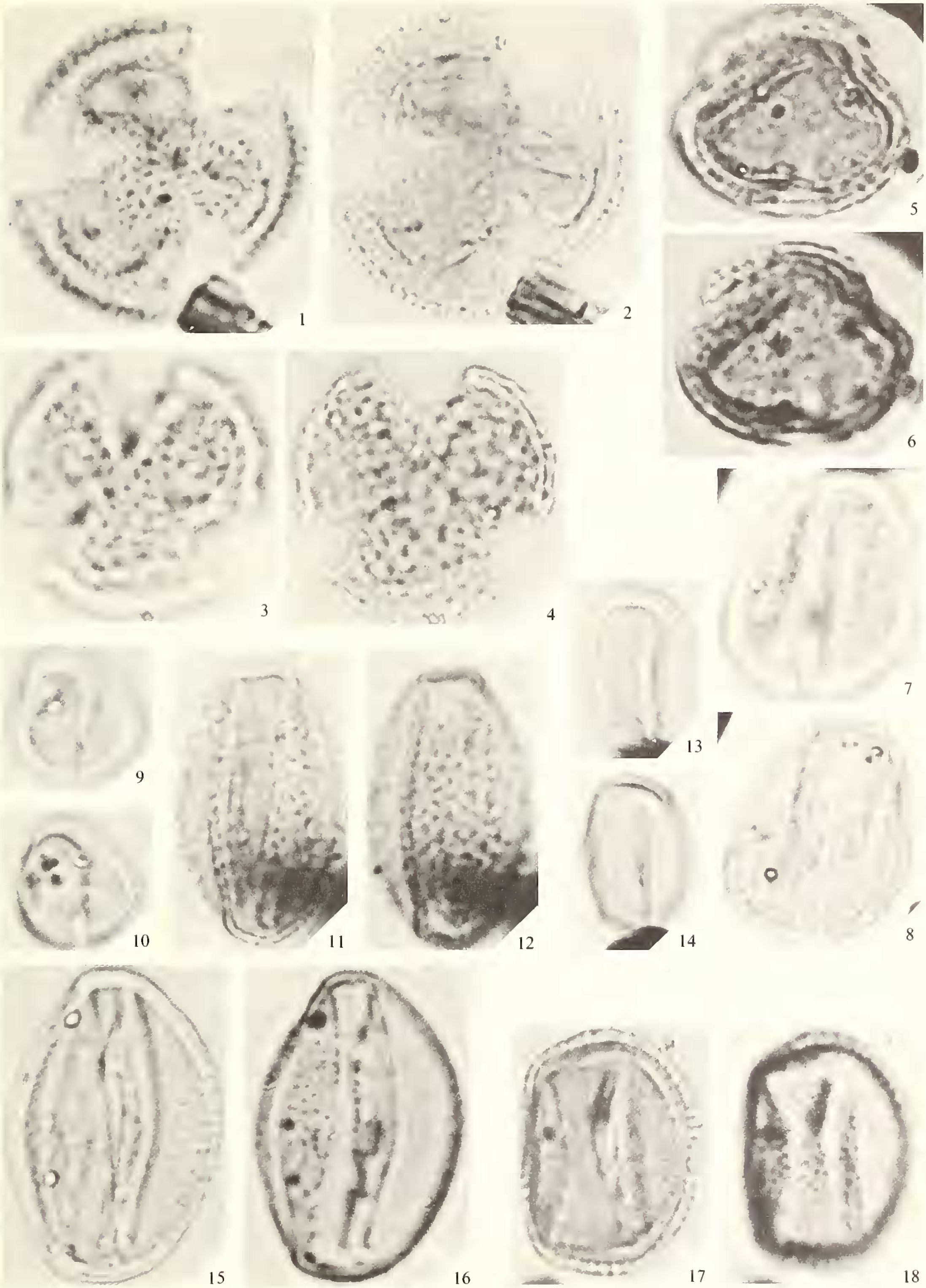
Orientation. Type material: P 50·0%, OA 50·0%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrences: Kemp (1968, 1970), Lower Albian (?*tardefurcata* Zone), England. *Known range*: ?*tardefurcata* Zone, Lower Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

EXPLANATION OF PLATE 91

All figures ×2000.

Figs. 1-2. *Retitricolpites amplifissus* sp. nov. Large specimen with inner central body; polar aspect; ECO 4, JL 184.1; 31.1, 111.6; 1, low focus to show ornament; 2, median focus to show inner central body.
Figs. 3-8. *Retitricolpites crassitransennus* sp. nov. 3-4, holotype; polar aspect; ECO 5, JL 209.1; 40.1, 101.0; 3, high focus to show ornament; 4, median focus. 5-6, oblique aspect; ECO 5, JL 209.1; 41.3, 108.8; 5, median focus; 6, low focus. 7-8, equatorial aspect; ECO 5, JL 209.3; 32.8, 103.5; 7, high focus; 8, median focus.
Figs. 9-10. *Retitricolpites exiguiexemplum* sp. nov. Holotype; oblique aspect; ECO 5, JL 209.1; 47.4, 099.1; 9, high focus; 10, median focus.
Figs. 11-12. CfB. *Retitricolpites georgensis* Brenner. Equatorial aspect; ECO 7, JL 191.1; 29.5, 097.8; 11, median focus; 12, low focus to show ornament.
Figs. 13-14. *Retitricolpites meumendum* sp. nov. Holotype; equatorial aspect; ECO 5, JL 209.3; 42.1, 108.8; 13, median focus; 14, low focus to show ornament.
Figs. 15-16. CfC. *Retitricolpites nemejci* (Pacltová). Equatorial aspect; ECO 5, JL 209.1; 44.4, 100.6; 15, median focus; 16, low focus.
Figs. 17-18. *Retitricolpites promiscuus* sp. nov. Holotype; specimen with lumina of varying size; equatorial aspect; ECO 5, JL 187.2; 26.4, 101.4; 17, median focus; 18, low focus to show ornament.



LAING, angiosperm pollen

Comments. The size distribution of the type material suggests that two species could be present, one with an average equatorial diameter of about 17 μm, the other of about 25 μm, but insufficient specimens have been found to show this conclusively. *Retitricolpites crassitransennus* differs by having slightly longer colpi, a generally finer-meshed microreticulum, wider muri, and undulating grain outlines. *R. promiscuus* has a generally more prolate shape and longer, narrower, more slit-like colpi. *R. vulgaris* Pierce, 1961 and *R. oblatoides* Pierce, 1961 were both inadequately described; either could be conspecific with this species. *Tricolpopollenites platyreticulatus* Groot, Penny and Groot, 1961 is a more coarsely reticulate form. *Tricolpites* sp. 2 of Agasie (1969) is, on average, a rather larger form, with a more straight-sided triangular outline and a microreticulum which becomes finer over the poles and at the colpus margins. *Tricolpites heusseri* Kimyai, 1966 seems to differ by having narrower colpi. *T. sagax* Norris, 1967 differs by sometimes being sub-prolate, by sometimes having a sub-granular exine, and by generally having narrower colpi. *Tricolpites* sp. A of Pacltová (1971) seems to differ in having a sexine of closely spaced (presumably discrete) pila rather than a microreticulum. *R. maximus* Singh, 1971 is larger and has thicker, more vermiculate muri and a more prolate shape. *T. reticulata* Cookson, 1947 is a generally rather larger form. *T. cooksonae* Dettmann, 1973 has a generally slightly coarser-meshed microreticulum with wider muri.

Retitricolpites crassitransennus sp. nov.

Plate 91, figs. 3–8

Description of sixteen specimens from samples ECO 1, ECO 5, and ECO 6. Oblate to prolate; circular to sub-triangular, quite deeply trilobate outline in polar view, elliptical to sub-circular in equatorial view. Three distinct colpi which gape at the equator, margins entire to slightly ragged. Clear exine stratification into unstructured nexine and microreticulate sexine; sexine of equal thickness to, or more commonly, thicker than nexine (very rarely sexine thinner than nexine). Microreticulum perfect; lumina usually of uniform size (rarely of varying size), irregularly shaped; muri sometimes of varying width, usually wider than lumina. Grain outlines undulating.

Holotype. Sample ECO 5, slide JL 209.1; 40.1, 101.0. Plate 91, figs. 3–4. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. PD 17–22 μm (3), ED 13 (19·3) 27 μm (16), PD/ED 1·0–1·4 (3), ET 1·0 (1·5) 2·1 μm (16), NT 0·2 (0·6) 1·1 μm (16), ST 0·5 (0·9) 1·2 μm (16), ST/NT 0·5 (2·2) 6·0 (16), LD 0·2 (0·4) 1·0 μm (16), MW 0·2 (0·6) 1·0 μm (16), LC 10–18 μm (3), LC/PD 0·7–0·8 (3), WC 2·0–6·0 μm (4), WC/ED 0·1–0·3 (4), DC 2·0–5·0 μm (4), DC/ED 0·1–0·2 (4).

Orientation. P 25·0%, E 18·8%, OA 56·3%.

Occurrence. This study: *rhotomagense* Zone, ?*costatus* Horizon to *jukes-brownei* Horizon, Middle Cenomanian.

Comments. See comments for *Retitricolpites amplifissus* and CfC. *R. nemejci* for distinction from these species. *Tricolpopollenites virgeus* Groot, Penny and Groot, 1961 has a coarser-meshed reticulum and is a little larger. *R. fragosus* Hedlund and Norris, 1968 is a little smaller and also differs in having the lumina reduced in size on the mesocolpia. *Tricolpites barrandei* Pacltová, 1971 is smaller and perhaps has a rather coarser-meshed microreticulum. *Foveotricolpites concinnus* Singh, 1971 differs by always being prolate, by having wider muri, and a coarser-meshed reticulum, and by being rather larger.

Retitricolpites exiguiexemplum sp. nov.

Plate 91, figs. 9–10; text-figs. 10–11

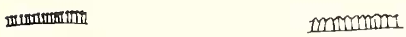
Description of nine specimens from samples ECO 3, ECO 5, and ECO 7. Spheroidal. Three distinct long deep colpi, most commonly narrow and slit-like, less commonly wider and gaping at the equator, margins entire. Clear exine stratification into unstructured nexine and microreticulate sexine; nexine and sexine usually of equal thickness (occasionally sexine thicker than nexine). Microreticulum usually perfect (occasionally imperfect with some free bacula); lumina of approximately uniform size and equidimensional shape; some specimens psilate over the poles. Grain outlines smooth to slightly indented.

Holotype. Sample ECO 5, slide JL 209.1; 47.4, 099.1. Plate 91, figs. 9–10. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. ED 7–12 μm (9), ET 0·8–1·8 μm (9), NT 0·2–0·9 μm (9), ST 0·4–0·9 μm (9), ST/NT 1·0–4·0 (9), LD $<$ 0·1–0·2 μm (9), MW $<$ 0·1–0·1 μm (9).

Orientation. OA 100·0%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *costatus* Horizon, *rhotomagense* Zone, Middle Cenomanian.



TEXT-FIG. 10. Cross-sections of sexine of *Retitricolpites subtilimaculatus* sp. nov. (*left*) and *R. exiguiexemplum* sp. nov. (*right*).

TEXT-FIG. 11. Holotypes of *Tricolpites albiensis* Kemp (*left*) and *Retitricolpites exiguiexemplum* sp. nov. (*right*), × 1000.

Comments. *Retitricolpites meumendum* is rather more prolate and has shallower colpi. Distinction from *R. subtilimaculatus* is sometimes difficult. The main difference seems to lie in the nature of the sexine; in the case of *R. subtilimaculatus* the sculptural elements stand up separately from each other to give a more indented outline (see text-fig. 10), whereas in *R. exiguiexemplum* the sculptural elements appear more fused, so that the outline is less indented. *Tricolpites albiensis* Kemp, 1968 is a similar form. It differs from this species in having less rounded 'lobes' (i.e. the area between the colpi—see text-fig. 11). Also, in the case of *T. albiensis* the sexine shows a tendency to thicken as it passes over the centre of the lobe (this feature is well shown in Kemp's (1968) pl. 81, fig. 7); such a tendency is less apparent in *R. exiguiexemplum*. Judging by Kemp's description, a further difference is that *T. albiensis* has a coarser-meshed microreticulum (LD 0·3–0·4 μm) which is imperfect: however, the holotype appears to have a perfect microreticulum of LD 0·2 μm. Further differences are that *T. albiensis* includes quite strongly prolate forms and is on average a little larger than *R. exiguiexemplum*. *Tricolpopollenites micromunus* Groot and Penny, 1960 was inadequately described; it might possibly be conspecific with this species. *Tricolpites reticulominutus* Jardiné and Magloire, 1965 differs from this species by being somewhat larger.

CfB. *Retitricolpites georgensis* Brenner, 1963

Plate 91, figs. 11–12; text-fig. 12

1963 *Retitricolpites georgensis* Brenner, p. 91, pl. 38, figs. 6–7.
1973 *Rousea georgensis* (Brenner) Dettmann, p. 14, pl. 2, figs. 16–17.

Description of eight specimens from samples ECO 1, ECO 3, ECO 5, and ECO 7. Sub-prolate to prolate; elliptical in equatorial view. Three distinct, narrow slit-like colpi, margins entire. Clear exine stratification into unstructured nexine and microreticulate sexine; sexine of equal thickness to, or thicker than, nexine (very rarely sexine thinner than nexine). Microreticulum perfect; lumina of varying size, usually becoming smaller towards the poles, irregularly shaped; muri sometimes of varying width, usually narrower than lumina. Grain outlines notched or coarsely indented at equator, becoming smoother towards the poles.

Dimensions. PD 15–26 μm (5), ED 10–16 μm (8), PD/ED 1·1–1·6 (5), ET 1·0–1·8 μm (8), NT 0·5–1·0 μm (8), ST 0·5–1·1 μm (8), ST/NT 0·5–2·8 (8), LD (least) 0·2–0·5 μm to (greatest) 1·0–2·5 μm (8), MW 0·2–0·8 μm (8), LC 9 (13·3) 20 μm (5), LC/PD 0·6 (0·7) 0·8 (5).

Orientation. P 0·0%, E 62·5%, OA 37·5%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrences: Brenner (1963), Albian, Maryland; Norris (1967), Late Albian, Alberta; Habib (1969), Middle Cretaceous, sea bed near the Bahamas; Paden Phillips and Felix (1971), Cenomanian, Louisiana; Playford (1971), Middle and ?Late Albian, Saskatchewan and Manitoba; Singh (1971), Middle Albian to Cenomanian, Alberta; Azema, Durand and Médus (1972), Middle Cenomanian, France; Dettmann (1973), Late Albian and Cenomanian, eastern Australia. *Known range*: Albian and Cenomanian.

Comments. The specimens described by Brenner (1963) are quite similar, but are, on average, larger (PD 18 (26) 36 μm, ED 17 (22) 28 μm) and show a smaller range of variation in the lumina diameter (0·5–1·5 μm). See comments for *Retitricolpites crassitransennus* and *Retitricolpites* sp. 1 for distinction from these species. *R. sarthensis* differs by having a finer-meshed microreticulum, a thinner exine either with unclear stratification or a thinner nexine relative to the sexine, and finely indented grain outlines. *R. promiscuus* has a rather finer-meshed microreticulum and more finely indented grain outlines. CfC. *R. nemejci* differs by having generally rather longer colpi, a finer-meshed more regular microreticulum, a generally thinner exine, a thinner nexine as compared to the sexine, and more finely indented grain outlines.

Retitricolpites meumendum sp. nov.

Plate 91, figs. 13–14

Description of twelve specimens from sample ECO 5. Prolate to sub-prolate (? perhaps to prolate spheroidal); elliptical or sub-circular in equatorial view. Three generally distinct narrow slit-like shallow colpi, margins entire (rarely ragged). Exine usually clearly stratified into unstructured nexine and a sexine which is usually psilate at the poles and microreticulate elsewhere, exine stratification unclear in some specimens; sexine usually thicker than nexine. Microreticulum perfect but not strongly developed; lumina of approximately uniform size and equidimensional shape. Grain outlines smooth at poles, elsewhere very finely indented.

Holotype. Sample ECO 5, slide JL 209.3; 42.1, 108.8. Plate 91, figs. 11–12. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. PD 10–15 μm (8), ED 7 (9·3) 14 μm (12), PD/ED 1·3–1·9 (8), ET 0·4 (0·6) 1·1 μm (12), NT 0·1–0·2 μm (8), ST 0·3–0·9 μm (8), ST/NT 2·0–5·0 (8), LD < 0·1 (0·2) 0·4 μm (12), MW < 0·1 (0·1) 0·2 μm (12), LC 8 (9·5) 13 μm (8), LC/PD 0·6 (0·8) 0·9 (8).

Orientation. P 0·0%, E 66·7%, OA 33·3%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *rhotomagense* Zone (? *costatus* Horizon), Middle Cenomanian.

Comments. See comments for *Retitricolpites exiguiexemplum* for distinction from this species. CfC. *R. nemejci* is generally rather larger, is less commonly psilate at the poles, and has a more distinct microreticulum with generally wider muri. *R. subtilimaculatus* has rather deeper colpi, the microreticulum developed all over the grain, and a thicker exine.

CfC. *Retitricolpites nemejci* (Pacltová 1971) comb. nov.

Plate 91, figs. 15–16

1971 *Tricolpites němejci* Pacltová, p. 113, pl. 4, figs. 1–5; pl. 5, figs. 1–12; pl. 6, figs. 1–12.

Description of five specimens from sample ECO 5. Sub-prolate to prolate; elliptical in equatorial view. Three distinct parallel-sided colpi, margins entire. Clear exine stratification into unstructured nexine and microreticulate sexine (sexine very occasionally psilate at the poles); sexine thicker than nexine. Microreticulum perfect; lumina either of approximately uniform or of slightly varying size, irregularly polygonal in shape; muri often of varying width. Grain outlines finely indented (very occasionally smooth at the poles).

Dimensions. PD 16–24 μm (5), ED 9–16 μm (5), PD/ED 1·3–1·8 (5), ET 0·6–1·0 μm (5), NT 0·1–0·2 μm (5), ST 0·5–0·8 μm (5), ST/NT 4·0–7·0 (5), LD 0·1–0·4 μm (5), MW 0·2–1·0 μm (5), LC 12 (17·1) 22 μm (5), LC/PD 0·8 (0·8) 0·9 (5).

Orientation. E 100·0%.

Occurrence. This study: *dispar* Zone, Upper Albian to *rhotomagense* Zone (? *costatus* Horizon), Middle Cenomanian. Other occurrence: Pacltová (1971), Cenomanian, Bohemia. *Known range*: *dispar* Zone, Upper Albian and Cenomanian.

Comments. Some of the specimens figured by Pacltová (1971) are similar to the forms described here. Pacltová described the shape as being oblate to sub-prolate although some of her figured specimens are clearly prolate. Pacltová's specimens are, on average, rather larger (PD 23 (25) 28 μm) and have slightly coarser microreticula than the specimens found in this study. See comments for CfB. *Retitricolpites georgensis* and *R. meumendum* for distinction from these species. *R. crassitransennus* differs by being more spheroidal and by having slightly shorter colpi, a generally slightly coarser-meshed microreticulum, a generally thicker exine, and undulating grain outlines. *R. promiscuus* has a coarser-meshed microreticulum, a generally thicker exine, nexine and sexine typically of about equal thickness, and possibly has narrower colpi. *Foveotricolpites sphaeroides* Pierce, 1961 and *Quercoïdites* sp. of Azéma and Ters (1971) seem to be similar forms but both were inadequately described for comparative purposes. *Retitricolpites* sp. B of Hedlund and Norris (1968) also seems to be similar, but it was undescribed.

Retitricolpites promiscuus sp. nov.

Plate 91, figs. 17–18; Plate 92, figs. 1–2

Description of fifty-four specimens from samples ECO 1, ECO 2, ECO 5, and ECO 6. Spheroidal to prolate; sub-circular trilobate outline in polar view, elliptical in equatorial view. Three, usually distinct, slit-like (occasionally more gaping) colpi, margins entire or slightly ragged. Clear exine stratification into unstructured nexine and microreticulate sexine; nexine and sexine usually of about equal thickness (occasionally sexine a little thicker than nexine). Microreticulum perfect; lumina of varying size in about two-thirds of the specimens examined, and of more uniform size in about one-third of the specimens, irregularly polygonal in shape. Grain outlines finely indented.

Holotype. Sample ECO 5, slide JL 187.2; 26.4, 101.4. Plate 91, figs. 17–18. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. Type material: PD 12 (17·4) 23 μm (27) s3·4 μm, ED 8 (13·7) 21 μm (54) s3·5 μm, PD/ED 1·0 (1·4) 1·8 (27), ET 1·0 (1·4) 2·0 μm (54), NT 0·3 (0·6) 1·0 μm (54), ST 0·5 (0·7) 1·0 μm (54), ST/NT 0·8 (1·3) 3·3 (54), LD (least) 0·1 (0·2) 0·5 μm to (greatest) 0·1 (0·6) 2·0 μm (54), MW 0·1 (0·2) 0·3 μm (54), LC 8 (11·6) 18 μm (26), LC/PD 0·5 (0·7) 0·9 (26), WC 0·5–2·0 μm (2), WC/ED < 0·1–0·1 (2), DC 1·0–1·5 μm (2), DC/ED 0·1 (2). Other material: Samples JOU 1, JOU 2, and JOU 4, PD 12 (14·6) 20 μm (13), ED 8 (10·1) 14 μm (17); Samples JOU 8, JOU 16, and JOU 17, PD 13–20 μm (6), ED 10–17 μm (8).

Orientation. Type material: P 3·7%, E 50·0%, OA 46·3%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. See comments for *Retitricolpites amplifissus*, CfB *R. georgensis*, and CfC. *R. nemejci* for distinction from these species. *R. sarthensis* differs by having a generally thinner exine, either with unclear exine stratification or with the nexine rather thinner than the sexine.

Retitricolporites insolitimorus is superficially similar but it is sometimes tetrahedral in shape. Further, it does not always have three colpi, but has pores, and tends to have a thicker nexine than sexine, and shorter colpi.

The specimens described as *Tricolpopollenites retiformis* Pflug and Thomson by Groot, Penny and Groot (1961) might be the same species, but they are inadequately described for a close comparison (Thomson and Pflug's (1953) original description also is inadequate for comparative purposes). *T. haraldii* Manum, 1962 is a larger form with a thinner nexine relative to the sexine. *Retitricolpites prosimilis* Norris, 1967 differs by having a decrease in lumina diameter towards the poles and a generally thinner exine. *Tricolpites variabilis* Burger, 1970 differs in having a generally slightly

EXPLANATION OF PLATE 92

All figures ×2000.

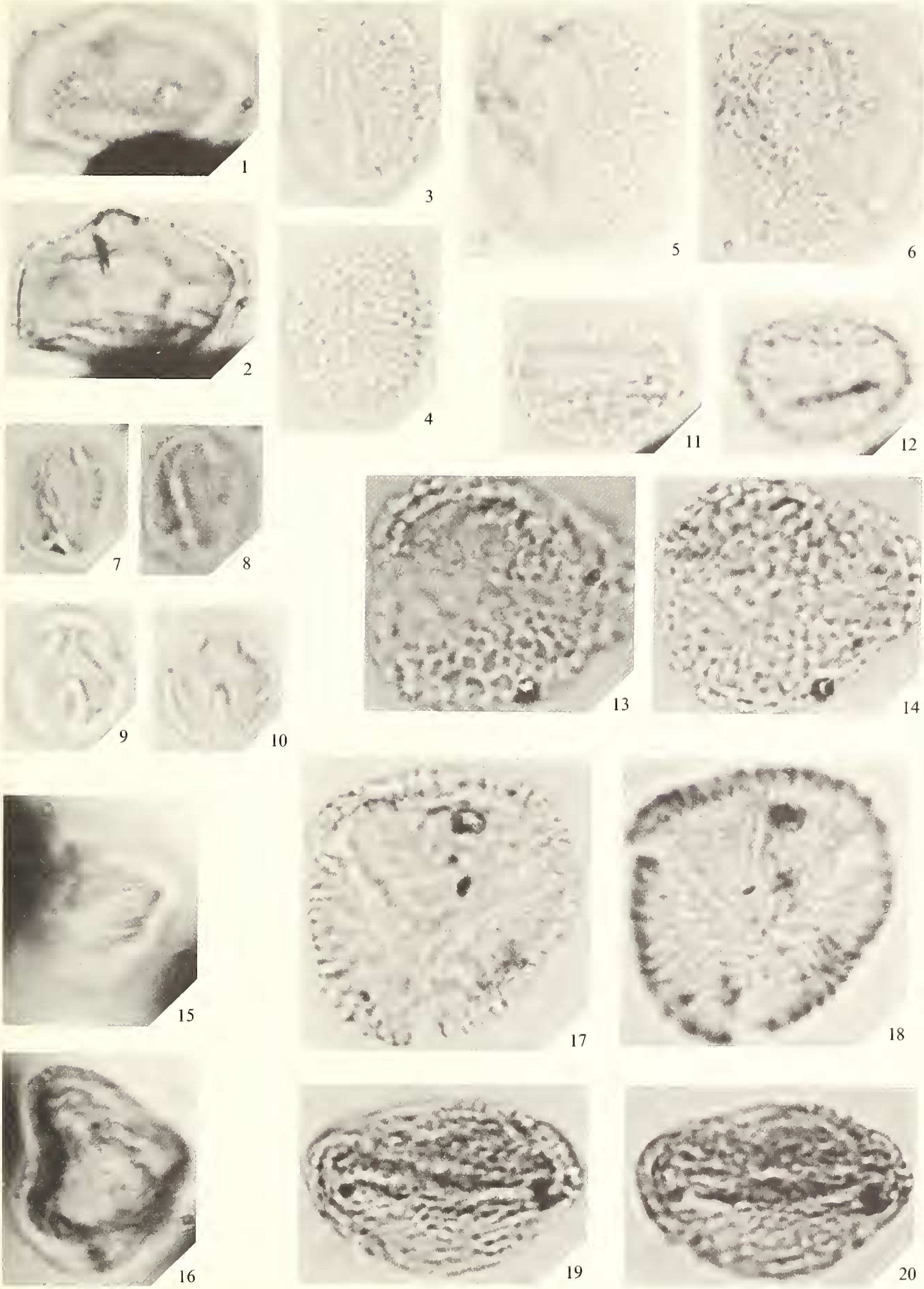
Figs. 1–2. *Retitricolpites promiscuus* sp. nov. Specimen with lumina of approximately uniform size; equatorial aspect; ECO 5, JL 209.1; 33.9, 097.7; 1, high focus to show ornament; 2, median focus.

Figs. 3–6. *Retitricolpites sarthensis* sp. nov. 3–4, holotype; equatorial aspect; ECO 5, JL 187.3; 53.6, 105.9; 3, high focus; 4, median focus. 5–6, oblique aspects; PUN 1, JL 106.3; 40.4, 097.9; 5, median focus; 6, low focus.

Figs. 7–10. *Retitricolpites subtilimaculatus* sp. nov. 7–8, holotype; equatorial aspect; ECO 5, JL 187.2; 32.1, 103.3; 7, high focus; 8, median focus. 9–10, oblique aspect; ECO 5, JL 209.2; 35.1, 105.7; 9, high focus; 10, median focus.

Figs. 11–14. *Retitricolpites* sp. 1. 11–12, equatorial aspect; ECO 5, JL 209.2; 52.5, 105.1; 11, median focus; 12, high focus to show ornament. 13–14, oblique aspect; ECO 5, JL 187.2; 54.5, 111.6; 13, high focus to show ornament; 14, median focus.

Figs. 15–20. CfC. *Striatopollis sarstedtensis* Krutzsch. 15–16, oblique aspect; ECO 5, JL 187.2; 51.5, 099.8; 15, high focus; 16, median focus. 17–18, polar aspect; ECO 5, JL 187.2; 25.0, 100.5; 17, median focus; 18, high focus to show ornament, note the development of the polar microreticulum. 19–20, equatorial aspect; ECO 5, JL 209.2; 28.1, 111.8; 19, high focus to show ornament, note the cross pieces linking the muri; 20, median focus.



LAING, angiosperm pollen

thinner exine, the nexine thinner than the sexine, and by having narrow costae bordering the colpi. *T. brnicensis* Pacltová, 1971 differs by sometimes being oblate, by being generally larger, and by always having more or less uniform-sized lumina.

Retitricolpites sarthensis sp. nov.

Plate 92, figs. 3–6

1971 *Tricolpites vulgaris* (Pierce) Pacltová, p. 113, pl. 3, figs. 6–13.

Description of forty-four specimens from samples ECO 2, ECO 5, ECO 6, and ECO 7. Prolate spheroidal to prolate; elliptical to circular in equatorial view. Three narrow slit-like (occasionally more gaping) colpi, margins entire (occasionally slightly ragged). Exine thin, microreticulate, stratification often unclear (specimens with thicker exines show stratification into unstructured nexine and thicker microreticulate sexine). Microreticulum perfect; lumina of varying size, irregularly polygonal in shape. Grain outlines finely indented.

Holotype. Sample ECO 5, slide JL 187.3; 53.6, 105.9. Plate 92, figs. 3–4. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. Type material: PD 13 (14·6) 18 μm (26) s1·7 μm, ED 7 (11·8) 19 μm (44) s3·4 μm, PD/ED 1·1 (1·4) 1·9 (26), ET 0·4 (0·8) 1·2 μm (44), NT (where determinable) 0·1 (0·2) 0·2 μm (21), ST (where determinable) 0·8 (0·9) 1·0 μm (21), ST/NT (where determinable) 4·0 (5·8) 9·0 (21), LD (least) 0·1 (0·3) 0·5 μm to (greatest) 0·4 (1·0) 2·0 μm (44), MW 0·1 (0·2) 0·5 μm (44), LC 8 (11·2) 16 μm (26), LC/PD 0·6 (0·8) 0·9 (26). Other material: Sample PUN 1, PD 16 (19·9) 24 μm (11), ED 10 (14·7) 19 μm (16); Sample WOR 1, PD 17–23 μm (6), ED 9–16 μm (6).

Orientation. Type material: P 0·0%, E 61·4%, OA 38·6%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrence: Pacltová (1971), Cenomanian, Bohemia. *Known range*: *inflatum* Zone, Upper Albian to Cenomanian.

Comments. See comments for CfB. *Retitricolpites georgensis*, *R. promiscuus*, and *Retitricolpites* sp. 1 for distinction from these species. The form described by Pacltová (1971) as *Tricolpites vulgaris* (Pierce) is very similar, but is a little larger (PD 20–28 μm, ED 18–24 μm). *R. vulgaris* Pierce, 1961 was too briefly described for a close comparison, but it does seem to be a larger form, perhaps with a thicker exine and wider colpi. *R. minutus* Pierce, 1961 also seems to be a similar form. It also was inadequately described for a close comparison; however, it does seem to differ from this species by having wider colpi with slightly thickened margins. *R. prosimilis* Norris, 1967 differs by usually having a reduced ornament on the apocolpia. Norris noted, however, that some of his specimens lacked this feature and that these might represent a separate species; perhaps the latter belong to *R. sarthensis*. *Tricolpopollenites microreticulatus* Takahashi, 1961 is superficially similar; unfortunately, it was inadequately described for a close comparison.

Retitricolpites subtilimaculatus sp. nov.

Plate 92, figs. 7–10; text-fig. 10

Description of seven specimens from sample ECO 5. Spheroidal to prolate; elliptical to circular in equatorial view. Three colpi, narrow and slit-like or wide and gaping at the equator, quite deep, margins entire (occasionally slightly ragged), sometimes rather indistinct. Clear exine stratification into unstructured nexine and microreticulate sexine; sexine thicker than nexine. Microreticulum perfect; lumina of about uniform size and equidimensionally shaped. Grain outlines finely indented.

Holotype. Sample ECO 5, slide JL 187.2; 32.1, 103.3. Plate 92, figs. 7–8. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. PD 11–12 μm (2), ED 8–12 μm (7), PD/ED 1·0–1·4 (2), ET 1·0–1·7 μm (7), NT 0·2–0·8 μm (7), ST 0·7–0·9 μm (7), ST/NT 1·1–4·0 (7), LD 0·1–0·2 μm (7), MW 0·1 μm (7), LC 7–10 μm (2), LC/PD 0·6–0·8 (2).

Orientation. P 0·0%, E 28·6%, OA 71·4%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *rhotomagense* Zone (? *costatus* Horizon), Middle Cenomanian.

Comments. See comments for *Retitricolpites exiguiexemplum* and *R. meumendum* for distinction from these species. *Tricolpopollenites minutus* Brenner, 1963 is a very similar form which perhaps differs in having a generally slightly thinner exine and possibly also in having smoother or less indented grain outlines. *Tricolpites albiensis* Kemp, 1968 differs by being somewhat larger and by having much more closely-spaced sexinal sculptural elements, such that the grain outlines are more or less smooth.

Retitricolpites sp. 1

Plate 92, figs. 11–14; text-fig. 12

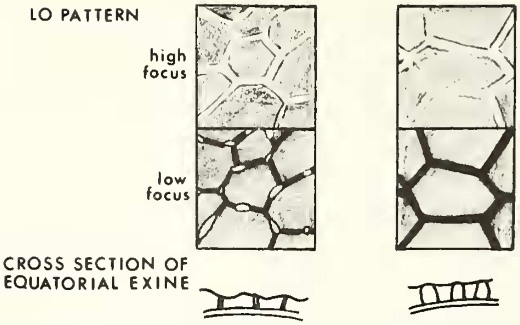
Description of seven specimens from sample ECO 5. Prolate spheroidal to prolate; sub-circular to elliptical in equatorial view. Three colpi, usually narrow and slit-like but occasionally wide and gaping at the equator, margins more commonly entire than ragged and sometimes a little thickened, sometimes indistinct. Clear exine stratification into unstructured nexine and a sexine composed of bacula which support a microreticulum; nexine usually thinner than sexine (very rarely nexine and sexine of about equal thickness). Microreticulum usually imperfect (often with some discrete bacula) but sometimes perfect; lumina of varying size, irregularly polygonal in shape. Grain outlines indented.

Dimensions. Sample ECO 5: PD 15–17 μm (3), ED 11–20 μm (7), PD/ED 1·1–1·4 (3), ET 1·0–1·5 μm (7), NT 0·2–0·5 μm (7), ST 0·5–1·0 μm (7), ST/NT 1·0–4·5 (7), LD (least) 0·2–0·5 μm to (greatest) 1·5–2·5 μm (7), MW 0·1–0·2 μm (7), LC 7–13 μm (3), LC/PD 0·5–0·8 (3). Samples JOU 1 and JOU 4: PD 16–23 μm (4), ED 12–17 μm (6).

Orientation. Sample ECO 5: P 0·0%, E 42·9%, OA 57·1%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *costatus* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. Since only a few specimens of this type have been found from any one locality, and of these some are not well preserved, I have not attempted to erect a new species to accommodate them. *Retitricolpites sarthensis* differs by having a constantly perfect, rather finer-meshed microreticulum. CfB. *R. georgensis* differs by having a microreticulum composed of solid muri which are in continuous contact with the nexine thus giving a different LO pattern (see text-fig. 12). The microreticulum of this species is also constantly perfect. *Tricolpopollenites platyreticulatus* Groot, Penny and Groot, 1961 seems to differ by having a constantly perfect microreticulum which (judging from the figures) continues down to the nexine rather than being supported on bacula. *T. macroreticulatus* Groot and Groot, 1962 seems to differ by being rather larger, by having the colpi bordered by a margo, and an apparently constantly perfect microreticulum which is in continuous contact with the nexine. *T. virgeus* Groot, Penny and Groot, 1961 seems to differ in having the microreticulum made up of,



TEXT-FIG. 12. LO patterns and cross-sections of equatorial exine of *Retitricolpites* sp. 1 (*left*) and CfB. *R. georgensis* Brenner (*right*).

rather than supported by, bacula. *Tricolpites* sp. 1 of Kemp (1968) differs by having a perfect microreticulum which tends to detach from the nexine. *R. marginatus* van Hoeken-Klinkenberg, 1966 differs by being larger, by having a rather coarser-meshed microreticulum which is reduced along the colpus margins, and by having a thicker exine.

Genus STRIATOPOLLIS Krutzsch, 1959

1959 *Striatopollis* Krutzsch, p. 142.
1962 *Striopollis* Rouse, p. 212.

Type species. *Striatopollis sarstedtensis* Krutzsch, 1959, p. 143, pl. 34, figs. 1–24; text-fig. 12.

CfC. *Striatopollis sarstedtensis* Krutzsch, 1959

Plate 92, figs. 15–20; Plate 93, fig. 1

1959 *Striatopollis sarstedtensis* Krutzsch, p. 143, pl. 34, figs. 1–24; text-fig. 12.

EXPLANATION OF PLATE 93

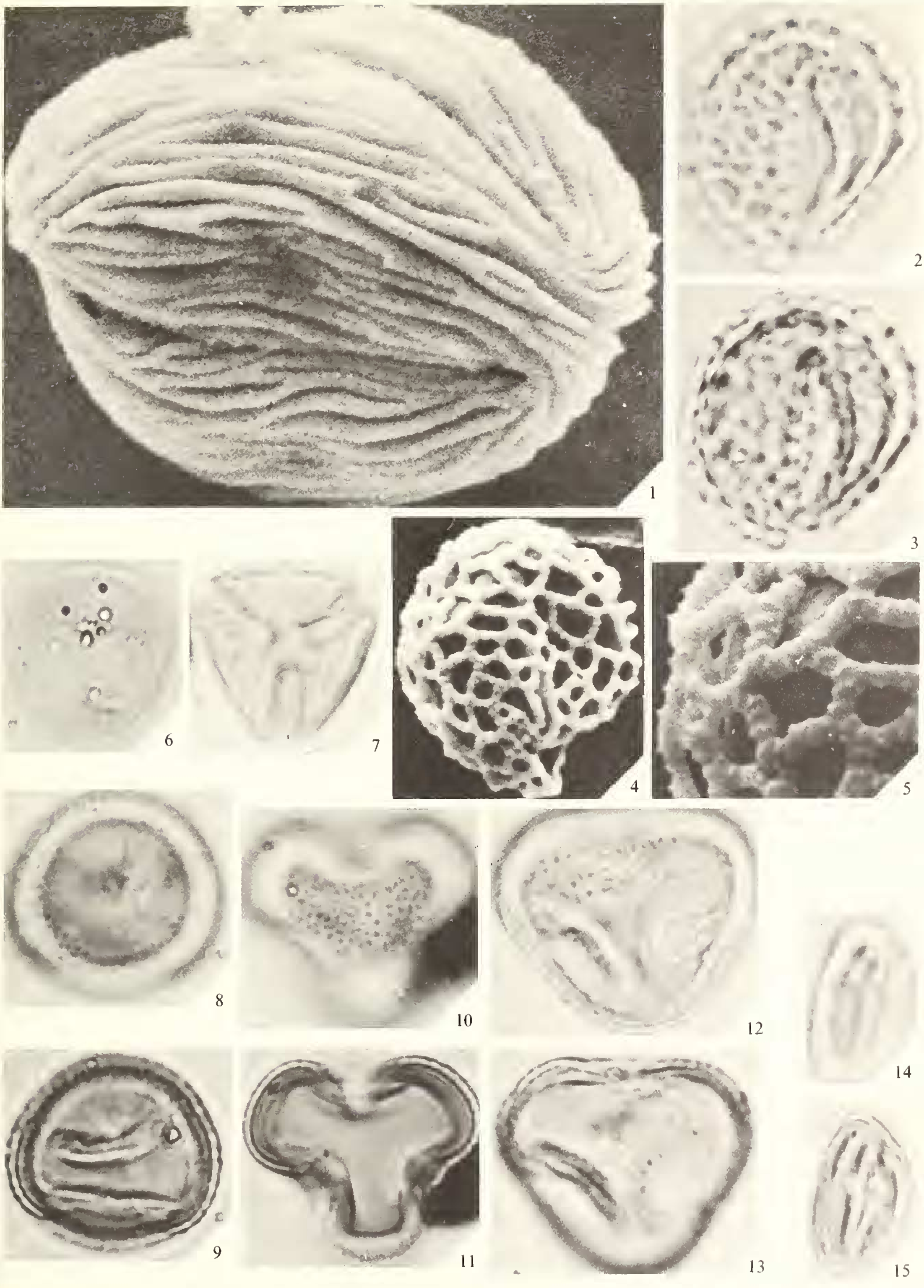
Fig. 1. CfC. *Striatopollis sarstedtensis* Krutzsch. Scanning electron micrograph; near equatorial aspect; ECO 5, stub JL 8; 335714; ×5000.

Figs. 2–5. CfA. *Liliacidites peroreticulatus* (Brenner). 2–3, distal polar aspect; ECO 4, JL 184.1; 32.0, 110.6; 2, high focus to show ornament; 3, median focus; ×2000. 4–5, scanning electron micrographs; oblique aspect; ECO 5, stub JL 8; 224803; 4, ×2000; 5, ×5000.

Figs. 6–7. *Psilatricolporites complanatius* sp. nov. 6, holotype; syncolpate specimen; polar aspect; ECO 5, JL 209.1; 30.2, 101.6; median focus; ×2000. 7, specimen with small apocolpia; polar aspect; ECO 5, JL 209.2; 38.9, 103.1; median focus; ×2000.

Figs. 8–13. *Retitricolporites insolitimorus* sp. nov. 8–9, holotype; ellipsoidal specimen with two colpi (one apparently with no pore) and two pores (one apparently not associated with a colpus); equatorial aspect; ECO 5, JL 209.2; 23.7, 105.0; 8, high focus to show ornament and pore; 9, median focus; ×2000. 10–11, ellipsoidal specimen with three pores and three colpi; polar aspect; PUN 1, JL 106.3; 39.3, 103.0; 10, high focus to show ornament; 11, median focus; ×2000. 12–13, tetrahedral specimen with three colpi and three pores; ECO 1, JL 179.1; 35.2; 110.4; 12, median focus; 13, low focus; ×2000.

Figs. 14–15. *Retitricolporites ecommoyensis* sp. nov. Holotype; equatorial aspect; ECO 5, JL 209.2; 32.4, 106.9; 14, high focus; 15, median focus; ×2000.



LAING, angiosperm pollen

Description of five specimens from sample ECO 5. Spheroidal to prolate; triangular trilobate outline in polar view, sub-circular to elliptical in equatorial view. Three slit-like colpi, margins entire, angul-aperturate, sometimes syncolpate. Clear exine stratification into unstructured nexine and striate or striato-microreticulate sexine; sexine thicker than nexine. Muri and striae tend to parallel the polar axis, sometimes anastomosing and occasionally (especially near the poles) linked by cross pieces to form a microreticulum; S.E.M. observation shows the muri to bear small cones.

Dimensions. PD 15–24 μm (3), ED 10–23 μm (5), PD/ED 1·4–1·6 (3), ET 1·1–1·6 μm (5), NT 0·2–0·6 μm (5), ST 0·7–1·0 μm (5), ST/NT 1·4–4·5 (5), LD 0·3 μm (1), MW 0·2–0·5 μm (5), W striae 0·2–0·5 μm (5), number of muri between each pair of colpi 7–19 (4), LC 11–17 μm (2), LC/PD 0·7–0·8 (2), WC 0·2 μm (1), WC/ED < 0·1 (1), DC 1·0 μm (1), DC/ED < 0·1 (1).

Orientation. P 20·0%, E 60·0%, OA 20·0%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *costatus* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrences: Krutzsch (1959), Lower Paleocene, G.D.R.; Groot and Groot (1962), Cenomanian, Portugal. *Known range*: *inflatum* Zone, Upper Albian to Lower Paleocene.

Comments. None of the specimens described by Krutzsch (1959) seems to show the development of a polar microreticulum.

Striatopollis cf. *paraneus* (Norris) in Dettmann (1973) differs by having 'ropy' muri (under S.E.M. observation).

Subturma PTYCHOTRIPORINES Naumova emend. Potonié, 1960

As with the tricolpates, the genera of van der Hammen (1956) are used as they are the most convenient for light microscope studies.

Genus PSILATRICOLPORITES van der Hammen ex van der Hammen and Wymstra, 1964

1956 *Psilatricolporites* van der Hammen, p. 91.
1964 *Psilatricolporites* van der Hammen ex van der Hammen and Wymstra, p. 236.

Type species. Psilatricolporites operculatus van der Hammen and Wymstra, 1964, p. 236, pl. 1, fig. 13.

Psilatricolporites complanatius sp. nov.

Plate 93, figs. 6–7

Description of nine specimens from samples ECO 5 and ECO 7. Strongly oblate; triangular or rounded triangular, usually quite shallowly trilobate outline in polar view. Three distinct long gaping (less commonly more slit-like) colpi, margins entire but usually faint, angul-aperturate, sometimes syncolpate; single equatorial pore in each colpus, often rather unclear. No clear exine stratification. Psilate.

Holotype. Sample ECO 5, slide JL 209.1; 30.2, 101.6. Plate 93, fig. 6. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. PD *c.* 1·5 μm (1), ED 13–15 μm (9), PD/ED *c.* 0·1 (1), ET 0·4–0·8 μm (9), WC 1·5 (2·7) 6·0 μm (9), WC/ED 0·1 (0·2) 0·4 (9), DC 0·0 (0·6) 1·5 μm (9), DC/ED 0·0 (< 0·1) 0·1 (9), pore diameter 1·0 (2·4) 4·5 μm (8).

Orientation. P 100·0%.

Occurrence. This study: *carcitanensis* Horizon, *mantelli* Zone, Lower Cenomanian to *costatus* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. Tricolporopollenites orbiculatus Groot, Penny and Groot, 1961 differs from this species by being slightly prolate. *Tricolporopollenites* sp. S. CI. 215 of Jardiné and Magloire (1965) has a more sub-spherical shape. *Tricolporopollenites* sp. S. CI. 141 of Jardiné and Magloire (1965) is larger, has pores with annuli and perhaps has shorter colpi. *T. aliquantulus* Hedlund, 1966 has a more prolate shape. *Tricolporopollenites* sp. B of Brenner (1968) has much shorter colpi. *Nyssapollenites albertensis* Singh, 1971 differs by having rim-like thickenings around the pores, and by having much shorter colpi.

Genus RETITRICOLPORITES van der Hammen ex van der Hammen and Wymstra, 1964

1956 *Retitricolporites* van der Hammen, p. 93.
1964 *Retitricolporites* van der Hammen ex van der Hammen and Wymstra, p. 235.

Type species. Retitricolporites guianaensis van der Hammen and Wymstra, 1964, p. 235, pl. 3, figs. 1–2.

Retitricolporites ecommoyensis sp. nov.

Plate 93, figs. 14–15

Description of nine specimens from sample ECO 5. Prolate spheroidal to prolate; sub-circular to elliptical in equatorial view. Three distinct narrow slit-like colpi, margins entire and with nexinal thickening; single distinct equatorial pore in each colpus; many specimens have the colpi buckled out at the equator (i.e. they are tricolporoidate in the sense of Doyle 1969). Clear exine stratification into unstructured nexine and microreticulate sexine (sexine occasionally psilate at the poles); sexine generally thicker than nexine (except at colpus margins and sometimes at the poles), occasionally exine (particularly nexine) thickens at the poles. Microreticulum perfect; lumina of about uniform size and equidimensionally shaped. Grain outlines finely indented to smooth.

Holotype. Sample ECO 5, slide JL 209.2; 32.4, 106.9. Plate 93, figs. 14–15. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. PD 10–16 μm (8), ED 6–13 μm (9), PD/ED 1·1–1·7 (8), equatorial ET 0·5–1·2 μm (9), equatorial NT 0·1–0·4 μm (9), equatorial ST 0·4–0·8 μm (9), equatorial ST/NT 1·5–4·0 (9), LD $<$ 0·1–0·3 μm (9), MW $<$ 0·1–0·2 μm (9), LC 7 (9·4) 13 μm (8), LC/PD 0·6 (0·7) 0·8 (8), thickness of colpus margins 0·5–1·0 μm (9), pore diameter 0·2 (0·7) 1·2 μm (9).

Orientation. P 0·0%, E 88·9%, OA 11·1%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. Tricolporopollenites inaequalis Groot, Penny and Groot, 1961 is a larger form which seems to have unthickened colpus margins. *Tricolporopollenites* sp. S. CI. 428 of Jardiné and Magloire (1965) differs by its larger size and by the fact that it often occurs in tetrads. *Tricolporoidites minimus* Pacltová, 1971 has a rather thicker exine and a granulate nexine. *T. subtilis* Pacltová, 1971 differs in having a chagrenate exine.

Retitricolporites insolitimorus sp. nov.

Plate 93, figs. 8–13

Description of thirty-nine specimens from samples ECO 1, ECO 2, ECO 4, ECO 5, ECO 6, and ECO 7. Variable in shape, either ellipsoidal (oblate spheroidal to sub-prolate) or a more tetrahedral shape; ellipsoidal grains with triangular quite deeply trilobate outline in polar view, elliptical in equatorial view; tetrahedral grains with a more triangular outline. Tricolporate development often aberrant with up to three colpi which may or may not have pores, or up to three pores, some of which may not be associated with colpi (the apparent lack of a full complement of pores and/or colpi in some specimens may simply be caused by the aspect of these specimens). Ellipsoidal grains fossaperturate. Pores sometimes elongate parallel to the polar axis but more commonly approximately circular; colpi relatively short and deep. Clear exine stratification into unstructured nexine and microreticulate sexine; nexine most commonly thicker than sexine, less commonly nexine and sexine of about equal thickness, only rarely sexine thicker than nexine. Microreticulum perfect; lumina either of about uniform size and regularly polygonal shape, or of more varying size and irregularly polygonal shape. Grain outlines finely indented to almost smooth.

Holotype. Sample ECO 5, slide JL 209.2; 23.7, 105.0. Plate 93, figs. 8–9. Argiles noires, Ecommoy; *rhotomagense* Zone, Middle Cenomanian.

Dimensions. Type material: PD 13 (17·8) 22 μm (15), ED 9 (15·7) 22 μm (39) s3·7 μm, PD/ED 0·8 (1·1) 1·2 (15), ET 1·0 (1·5) 2·5 μm (39), NT 0·4 (0·9) 1·5 μm (39), ST 0·4 (0·6) 1·0 μm (39), ST/NT 0·3 (0·7) 2·3 (39), LD (when uniform) 0·1 (0·2) 0·4 μm (26), LD (when varying) (least) 0·1 (0·2) 0·2 μm to (greatest) 0·3 (0·9) 2·0 μm (13), MW 0·1 (0·2) 0·3 μm (39), LC 3 (10·0) 15 μm (15), LC/PD 0·2 (0·5) 0·8 (15), WC 2·0–5·0 μm (2), WC/ED 0·1–0·3 (2), DC 1·5–3·0 μm (2), DC/ED 0·1–0·2 (2), pore diameter (including W of elongate pores) 0·8 (2·3) 6·0 μm (39), L of elongate pores 3·0–7·5 μm (6). Other material: Sample JOU 15, PD 15–19 μm (5), ED 12–17 μm (5).

Orientation. Type material: P 5·1%, E 41·0%, OA 53·8%.

Occurrence. This study: *inflatum* Zone, Upper Albian to *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. See comments for *Retitricolpites promiscuus* for distinction from this species.

Tricolporopollenites microreticulatus Thomson and Pflug, 1953 differs by being on average rather larger and in not showing an aberrant tricolporate development and tetrahedral condition. *T. inaequalis* Groot, Penny and Groot, 1961 differs by having the nexine thinner than the sexine and in not showing an aberrant tricolporate development and tetrahedral condition. *T. subobscurus* Groot and Penny, 1960, *Retitricolporites crassicostatus* van der Hammen and Wymstra, 1964, and *Tricolporoidites bohemicus* Pacltová, 1971 all differ in not showing an aberrant tricolporate development and tetrahedral condition.

Turma POROSES Naumova emend. Potonié, 1960
Subturma TRIPORINES Naumova emend. Potonié 1960
Genus COMPLEXIOPOLLIS Krutzsch emend. Góczán, Groot, Krutzsch and Pacltová, 1967

1959 *Complexiopollis* Krutzsch, p. 134.
1967 *Complexiopollis* Krutzsch emend. Góczán *et al.*, p. 453.

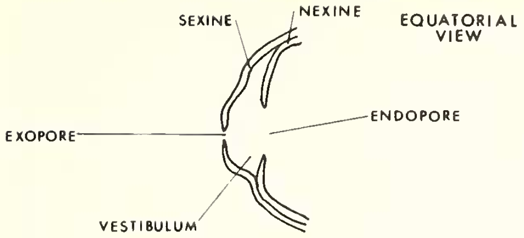
Type species. Complexiopollis praeatumescens Krutzsch, 1959, p. 135, pl. 31, figs. 39–54; text-fig. 6.

CfB. *Complexiopollis subtilis* (Krutzsch) Góczán, Groot, Krutzsch and Pacltová, 1967

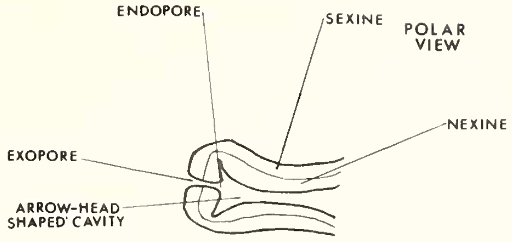
Plate 94, figs. 1–3; text-fig. 13

1959 *Latipollis subtilis* Krutzsch, p. 129, pl. 31, figs. 1–13; text-fig. 1.
1967 *Complexiopollis subtilis* (Krutzsch) Góczán *et al.*, p. 445.

Description of three specimens from sample WOR 1. Sub-oblate; elliptical in equatorial view, strongly



TEXT-FIG. 13. Pore structure of CfB. *Complexiopollis subtilis* (Krutzsch).



TEXT-FIG. 14. Pore structure of *Triporopollenites curtisi* sp. nov.

three-rayed shape in polar view. Three pores, often unclear, seemingly with faint vestibula (see text-fig. 13), angul-aperturate. Exine stratified into unstructured nexine and a sexine with a rather rough surface; nexine and sexine of about equal thickness. Grain outlines rather irregular.

Dimensions. PD 13–14 μm (2), ED 15–17 μm (3), PD/ED 0·8–0·9 (2), ET 1·0–1·2 μm (3), NT 0·5–0·6 μm (3), ST 0·5–0·6 μm (3), ST/NT 1·0 (3), exopore diameter 0·5–1·2 μm (3), exopore diameter/ED 0·03–0·07 (3), endopore diameter 0·5–1·2 μm (3), endopore diameter/ED 0·03–0·07 (3), vestibulum diameter 1·5–3·0 μm (3), vestibulum diameter/ED 0·10–0·17 (3), D of pores 2·0–2·1 μm (3), D of pores/ED 0·117–0·133 (3).

Orientation. P 0·0%, E 66·7%, OA 33·3%.

Occurrence. This study: *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian. Other occurrence: Krutzsch (1959), ?Upper Cenomanian and Turonian, Central Europe. *Known range*: *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian to Turonian.

Comments. Though the pore structure of the specimens described above is not clear, it does not appear to be as complicated as that described by Krutzsch (1959).

Genus TRIPOROPOLLENITES Thomson and Pflug, 1953

1953 *Triporopollenites* Thomson and Pflug, p. 82.

Type species. Triporopollenites coryloides Thomson and Pflug, 1953, p. 84, pl. 9, figs. 20–24.

Triporopollenites curtisi sp. nov.

Plate 94, figs. 4–7; text-fig. 14

Description of six specimens from sample WOR 1. Oblate: three-rayed or concave-sided triangular outline in polar view. Three, usually distinct, simple pores; exine sometimes a little thickened around the pores, and often a little constricted behind the endopore such that an arrow-head shaped or triangular cavity appears to be present behind the endopore (see text-fig. 14), angul-aperturate. Exine stratified into unstructured nexine and a sexine with a rather rough surface; nexine most commonly thinner than sexine, occasionally nexine and sexine of about equal thickness; exine stratification often rather unclear. Grain outlines rather irregular.

Holotype. Sample WOR 1, slide JL 236.1; 41.8, 100.5. Plate 94, figs. 4–5. Glauconitic Marl, Worbarrow Bay; probable *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Dimensions. ED 14–20 μm (6), ET 1·0–1·2 μm (6), NT 0·2–0·6 μm (6), ST 0·6–0·8 μm (6), ST/NT 1·0–1·4 (6), exopore diameter 0·2 (0·7) 1·1 μm (6), exopore diameter/ED 0·01 (0·03) 0·07 (6), endopore diameter 0·2 (0·7) 1·0 μm (6), endopore diameter/ED 0·01 (0·03) 0·07 (6), D of pore 1·0 (1·6) 2·0 μm (6), D of pore/ED 0·052 (0·084) 0·111 (6).

Orientation. P 50·0%, OA 50·0%.

Occurrence. This study: *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. Complexiopollis praeatumescens Krutzsch, 1959 differs in having more complex pores, more exine layers, a finely punctate to reticulate sculpture, and by being larger. *Latipollis vulgaris* Groot and Groot, 1962 has a more circular cavity behind the endopore (see text-fig. 2 of Groot and Groot). *Turonipollis helmigii* van Amerom, 1965 differs in having small atria and a granulate to reticulate sculpture. *Conclavipollis densilatus* Kimyai, 1966 is a larger form with a thicker exine and perhaps wider pores. *Triporopollenites pseudocanalis* Paden Phillips and Felix, 1971 is a larger form which has annuli around the pores and a more convex- (or at least not so strongly concave-) sided shape with protruding apices.

Triporopollenites worbarrowensis sp. nov.

Plate 94, figs. 8–11

Description of twelve specimens from sample WOR 1. Oblate; straight or slightly convex-sided triangular outline in polar view, equatorial apices slightly protruding. Three, usually distinct, simple pores; when damaged the pores occasionally have the appearance of short slightly gaping colpi with a V-shaped cross-section, angul-aperturate. Exine stratified into unstructured nexine and a sexine with a smooth or slightly rough surface; sexine slightly thicker than, or of equal thickness to, nexine (occasionally nexine slightly thicker than sexine); exine stratification occasionally unclear. Grain outlines smooth or slightly irregular.

Holotype. Sample WOR 1, slide JL 236.1; 26.0, 096.4. Plate 94, figs. 8–9. Glauconitic Marl, Worbarrow Bay; probable *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Dimensions. ED 16 (18·4) 23 μm (12), ET 0·7 (1·0) 1·3 μm (12), NT 0·3 (0·4) 0·6 μm (12), ST 0·4 (0·6) 1·0 μm (12), ST/NT 0·7 (1·5) 3·3 (12), exopore diameter 0·5 (1·2) 2·2 μm (11), exopore diameter/ED 0·02 (0·05) 0·10 (11), endopore diameter 0·5 (1·0) 2·0 μm (11), endopore diameter/ED 0·02 (0·04) 0·08 (11), D of pore 1·0 (1·3) 2·0 μm (11), D of pore/ED 0·052 (0·068) 0·111 (11).

Orientation. P 50·0%, OA 50·0%.

Occurrence. This study: *jukes-brownei* Horizon, *rhotomagense* Zone, Middle Cenomanian.

Comments. Triorites africanensis Jardiné and Magloire, 1965 differs in being rather larger.

EXPLANATION OF PLATE 94

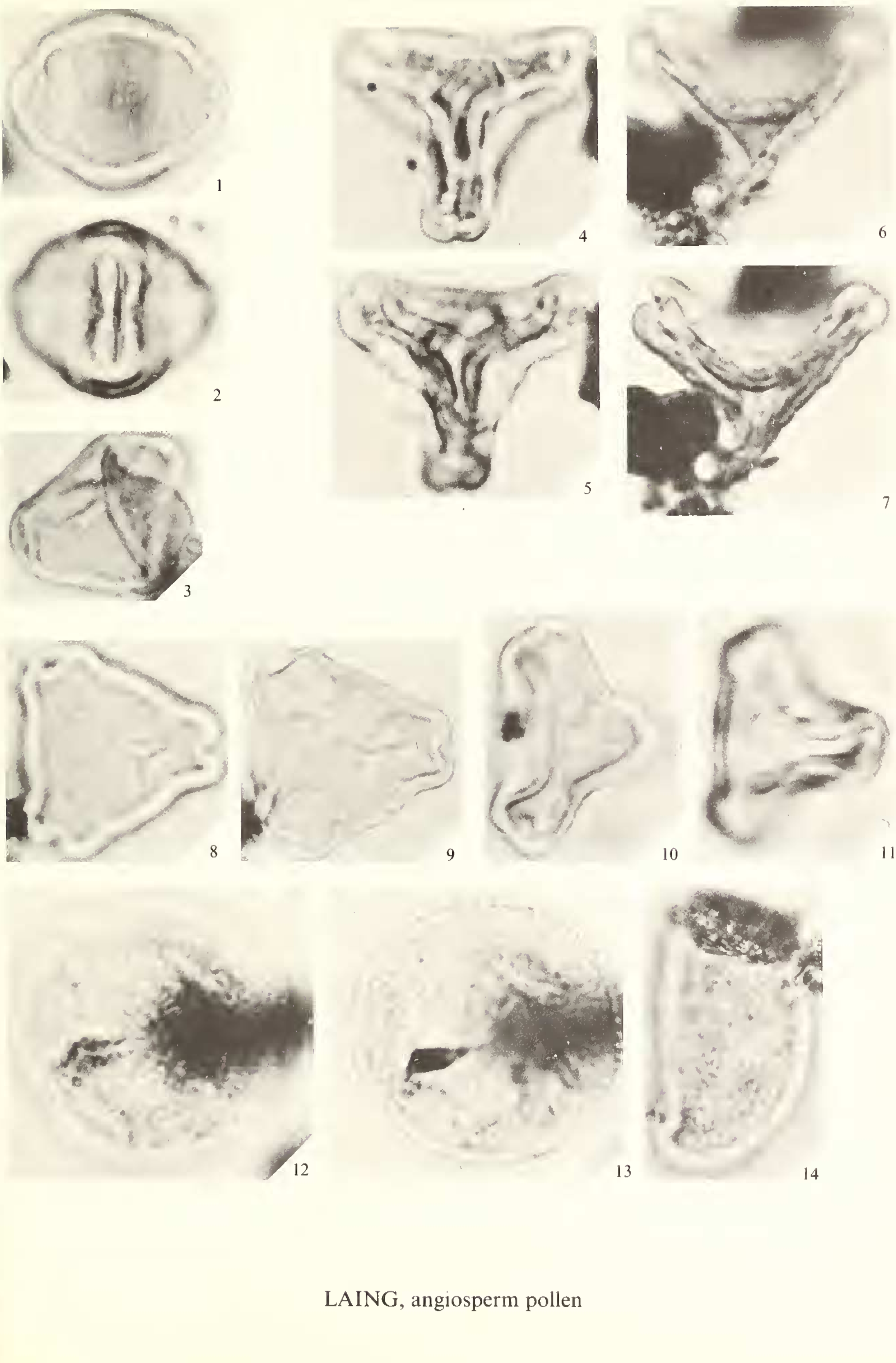
All figures ×2000.

Figs. 1–3. CfB. *Complexiopollis subtilis* (Krutzsch). 1–2, equatorial aspect; WOR 1, JL 236.1; 54.0, 095.9; 1, median focus; 2, low focus. 3, oblique aspect; WOR 1, JL 236.2; 33.1, 098.2; median focus.

Figs. 4–7. *Triporopollenites curtisi* sp. nov. 4–5, holotype; polar aspect; WOR 1, JL 236.1; 41.8; 100.5; 4, high focus; 5, median focus. 6–7, oblique aspect; WOR 1, JL 236.2; 51.6, 106.5; 6, high focus; 7, median focus.

Figs. 8–11. *Triporopollenites worbarrowensis* sp. nov. 8–9, holotype; polar aspect; WOR 1, JL 236.1; 26.0, 096.4; 8, high focus; 9, median focus. 10–11, oblique aspect; WOR 1, JL 238.1; 27.2, 111.2; 10, median focus; 11, low focus.

Figs. 12–14. CfB. *Asteropollis asteroides* Hedlund and Norris. 12–13, proximal polar aspect; ECO 5, JL 209.3; 32.6, 103.1; 12, high focus to show ornament; 13, median focus to show sulcus. 14, equatorial aspect; ECO 5, JL 209.3; 32.6, 101.9; high focus to show ornament.



LAING, angiosperm pollen

SEQUENCE OF POLLEN ASSEMBLAGES

Using the results of this study and the results of earlier workers (Couper 1958; Hughes 1958; Kemp 1968, 1970), it is possible to suggest a sequence of angiosperm pollen assemblages. Unfortunately, the data is as yet insufficient for the establishment of a zonal scheme, but I hope that this sequence will help others to make 'rule-of-thumb' stratigraphic assessments on material coming from this area. In another paper (Laing 1975), I have described a scheme which is, I hope, applicable over a wider area (perhaps over Europe and North America).

The approximate level of the earliest occurrence of each assemblage has been referred to the ammonite zonations of Spath (1923–1943) for the Albian and of Kennedy (1969) for the Cenomanian. The sequence of pollen assemblages and their approximate correlation with the ammonite zones are outlined on Table 2.

Liliacidites hughesii Assemblage.

Base. Within the Upper Barremian.

Diagnostic features. This assemblage is characterized by having reticulate and/or clavate monosulcate forms as the only angiospermous pollen present. In Britain and France there is only one angiospermous species at present known from this assemblage and that is *Liliacidites* (al. *Clavatipollenites*) *hughesii* (Couper 1958 emend. Kemp 1968) comb. nov. The base of the occurrence of this assemblage is thus defined by the first appearance of this species which occurs in the Upper Barremian (Hughes 1958).

Liliacidites rotundus–Retitricolpites amplifissus Assemblage

Base. Within the *Leymeriella tardefurcata* Zone (Lower Albian).

Diagnostic features. This assemblage is characterized by the presence of monosulcate and tricolpate forms; tricolporate forms may also be present but triporate forms are absent. Although *Retitricolpites sarthensis* may be present it is never the dominant angiosperm species (neither, for that matter, is it present in any abundance). In this area, the base of the occurrence of this assemblage may be defined by the first appearance of *Liliacidites rotundus* and *R. amplifissus*, which according to Kemp (1968, 1970) is in her sample F270. This is probably from the *tardefurcata* Zone of the Lower Albian. At this level, the only angiospermous species present are these two species and *L. hughesii*.

I have only studied the Upper Albian and Lower Cenomanian part of the time interval represented by this assemblage, and the evidence both from my work and that of Kemp (1968) is that *L. rotundus*, *R. amplifissus*, *R. promiscuus*, *Retitricolpites* sp. 1 and/or *Tricolpites albiensis* Kemp, 1968 are the dominant angiospermous species in the Upper Albian, and that *Retitricolporites insolitimorus* and/or *Retitricolpites amplifissus* may be the most abundant angiosperm species in the Lower Cenomanian. The time interval occupied by this assemblage is important in that it is the period during which reticulate, striate and psilate tricolpate, reticulate tri- to hexachotomosulcate (e.g. *Asteropollis*), and reticulate and psilate tricolporate forms first appear (for a fuller discussion of this see Laing 1975).

TABLE 2. Sequence of angiosperm pollen assemblages and their approximate correlation with the ammonite zonation of the mid-Cretaceous of southern Britain and northern France. (Ammonite zonation after Spath 1923–1943; and Kennedy 1969.)

STAGE	AMMONITE ZONE	ASSEMBLAGE OR FAUNAL HORIZON	POLLEN ASSEMBLAGE
MIDDLE CENOMANIAN	*Acanthoceras rhotomagense*	*Acanthoceras jukes-brownei*	*Triporopollenites worbarrowensis*
		Turrilites acutus	— ? — — — — — — *Retitricolpites sarthensis*
		Turrilites costatus	
LOWER CENOMANIAN	*Mantelliceras mantelli*	(uncharacterized)	— ? — — — — — — *Liliacidites rotundus–Retitricolpites amplifissus*
		Mantelliceras gr. *dixoni*	
		Mantelliceras saxbii	
		Hypoturrilites carcitanensis	
UPPER ALBIAN	*Stoliczkaia dispar*		
	Mortoniceras inflatum		
MIDDLE ALBIAN	*Euhoplites lautus*		
	Hoplites dentatus		
LOWER ALBIAN	*Douvilleiceras mammillatum*		
	Leymeriella tardefurcata	— ? — — — — — —	— — — — — — — —
APTIAN			*Liliacidites hughesii*
BARREMIAN	— ? — — — — —	— — — — — — — — —	— — — — — — — —

Retitricolpites sarthensis Assemblage

Base. Between the *Hypoturrilites carcitanensis* Assemblage horizon of the *Mantelliceras mantelli* Zone (Lower Cenomanian) and the *Turrilites costatus* Assemblage horizon of the *Acanthoceras rhotomagense* Zone (Middle Cenomanian).

Diagnostic features. This assemblage is characterized by the presence of either *Retitricolpites sarthensis* or *R. promiscuus* as the most abundant angiosperm species. When *R. promiscuus* is the most abundant species, then *R. sarthensis* is the next most abundant. *R. sarthensis* is always more abundant than *R. amplifissus.* Triporate grains are absent. *R. crassitransennus* makes its first appearance during the time interval represented by this assemblage and, apart from the possibility of the presence of this species, and the relative abundance of *R. sarthensis*, this assemblage is quite like the later (i.e. Lower Cenomanian) part of the *L. rotundus–R. amplifissus* Assemblage.

This assemblage occurs both in the base of the Glauconitic Marl at Punfield Cove and in the Argiles noires of Ecommoy.

Triporopollenites worbarrowensis Assemblage

Base. Between the *Turrilites costatus* and *Acanthoceras jukes-brownei* Assemblage horizons of the *A. rhotomagense* Zone (Middle Cenomanian).

Diagnostic features. The base of the occurrence of this assemblage is defined by the first appearance of triporate pollen. Three triporate species occur in the material which I have examined, *Triporopollenites worbarrowensis*, *T. curtisi*, and *Complexiopollis subtilis*, the first mentioned being the most abundant angiosperm species present.

This assemblage occurs in the base of the Glauconitic Marl at Worbarrow Bay. Although it would also be expected to occur in the base of the Glauconitic Marl at Lulworth Cove, I have found no triporate grains in this material. Indeed, this material is peculiar in being generally depleted in angiosperm pollen, such pollen being about six times as abundant (by comparison with the total spore/pollen content) in the material from Worbarrow Bay as it is in the material from Lulworth Cove.

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